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Lucie Arvy

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AN HISTORIC ERROR: CONFUSION BETWEEN RUYSCH'S SIRENIAN FOETUS (Ruysch, 1638-1731) AND THE NARWHAL FOETUS

* Thevet, F.A. Special features of Antarctic France, otherwise known as America and of several lands and islands discovered in our time. Antwerp: Plantin, 1558, p. 163.

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THE NARWHAL* (MONODON MONOCEROS L.)

by Lucie Arvy **

(Received for publication on May 25, 1978)

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* Called Tugálinn by the natives of Point Barrow, Alaska (Murdoch, 1885), Kialivak by the natives of Scoresby Sound (Tchernia, 1941) Naa-Hvalen or Nar-Hval by the Icelanders (Olafsen, 1772), Lighval in the Speculum regale.

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INTRODUCTION

The narwhal has known a certain notoriety since the 17th century because of its immediately apparent and unique peculiarity. In the Middle Ages, while this "sea unicorn" was not as famous as Jonas' whale (Hase, 1723), it was said nonetheless to be endowed with some astonishing properties. Powder from the "horn"* was a very rare commodity and commanded exorbitant prices. Many naturalists mentioned this "sea unicorn", hoping that they too would see it one day. One may be sure that Pontoppidan, the well-known bishop of Bergen, had never laid eyes on it, nor, for that matter, had Master Pomet, "the drug and spice merchant" in Paris who included the "sea unicorn" in his famous Histoire générale des drogues naturelles (General history of natural drugs).

Tulpi was the first to describe the narwhal skull (Fig. 1). It belonged to an animal that had washed up on the Ile of May (British Iles) in 1648. The narwhal was recognized as being related to the dolphin when Worm (1655) received a complete cranium from Iceland.

See page 1 a.

Fig. 1. Narwhal skull examined by Tulpi. First time the tooth was shown implanted in the skull. Top and bottom views. (In: 9th edition, 1672, of Observationum medicarum, Elsevier, Amsterdam)

* Along with bezoars found in the ibex, it was considered the most potent of alexipharmics, capable of preventing or curing poisoning by heavy metals, venom, etc.

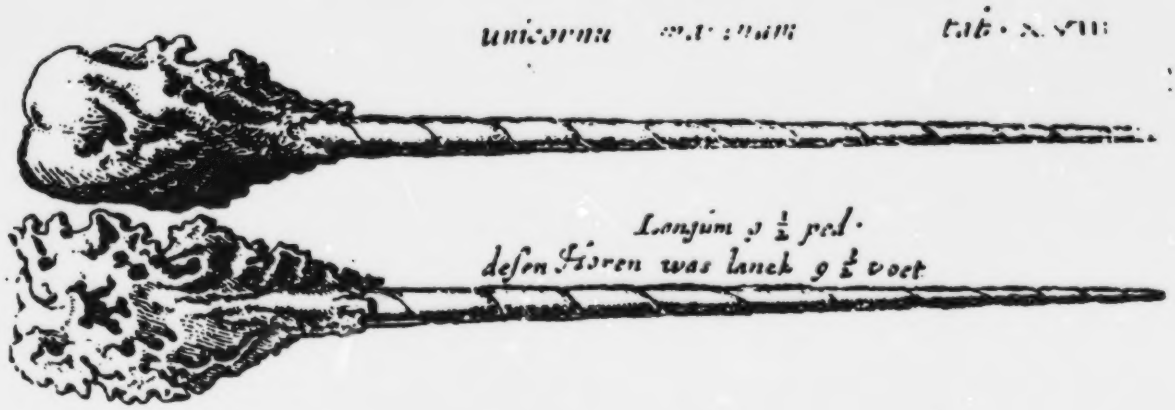

Fig. 1 — Photographie du crâne de narval, vu par Tulpi, première figuration de la dent implantée dans le crâne, vu de dessus et de dessous. (In : 9ème édition, 1672, de : *Observationum medicarum*, Elsevier, Amsterdam).

Fig. 1. Narwhal skull examined by Tulpi. First time the tooth was shown implanted in the skull. Top and bottom views. (In: 9th edition, 1672, of Observationum medicarum, Elsevier, Amsterdam)

One of the first representations of the narwhal we owe to Gudmonsson (1640), but the "nahvalur" depicted by this naturalist only remotely resembles the narwhal and that because of its "horn." Zorgdrager's interpretation (1723) is closer to the truth although his animal has two blowholes, four long fish fins (two of which are mediodorsal and two, medioventral), and a fringed tail that lies on a vertical axis (Fig. 2).

Fig. 2. The narwhal as seen by C. G. Zorgdrager (1723)

By comparison, Klein's narwhal (1741) has greater verisimilitude (Fig. 3). The bilobed tail has a regular margin and lies on a horizontal axis. The animal has a small mouth. The maxillary tooth emerges on the left side. There is only one blowhole. Numerous irregularly shaped and sized spots cover the animal's back and sides but do not appear on the abdomen. The anterior fin lies on a medioventral plane. There is no pectoral fin. The eye is set too far back. The blowhole is fringed anteriorly, but more than anything else, the proportions are all wrong: the animal is too short and fat.

See page 2 a.

Fig. 3. The narwhal as interpreted by J. T. Klein (1741).

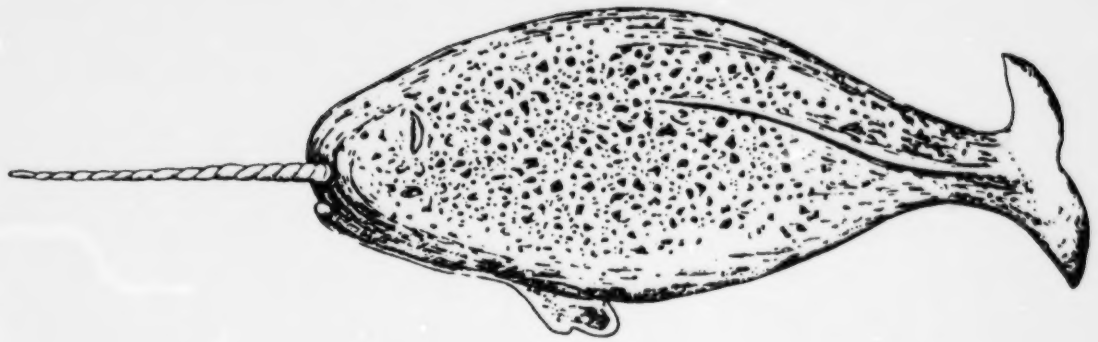

Fig. 3 — Le narval, vu par J.Th. Klein (1741).

Fig. 3. The narwhat as interpreted by J. T. Klein (1741).

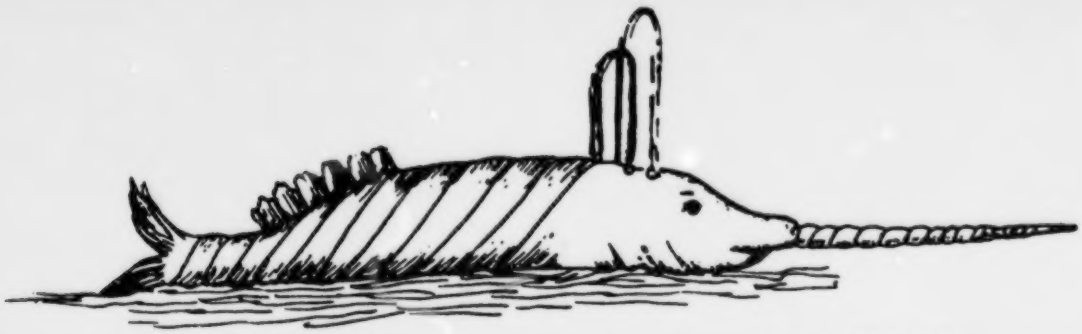

Fig. 4. The narwhal, as depicted by Pontoppidan (1755).

Pontopiddan's interpretation of the narwhal (1755) regressed to the point of becoming pure fantasy. His narwhal (Fig. 4) had two blowholes, a median tooth that grew out of a cylindrical snout and a fan-shaped dorsal fin with a serrated edge placed well to the rear. The vertical tail also fanned out. Willughbi's narwhal (1685) was less fanciful (Fig. 5). Actually, it was not until the 19th century (Fig. 6 and 7) that Fleming (1808) and Sowerby (1820) and even Kükenthal (1900) provided us with correct observations.

Representations of the narwhal foetus were late in coming and, for a while, were quite extraordinary. From Klein (1741) to Eales (1950), it was believed that Ruysch (1714) was the first to have observed the foetus of "Piscis Narwal" or "Unicornu Groenlandici." The foetus he examined was in fact radically different from a narwhal foetus and could have belonged only to a sirenian (Arvy, 1978). It was not until 1898 (Kükenthal) that the foetus was correctly represented.

The various names assigned to the animal signaled the state of uncertainty of our knowledge. The list includes De monocerote (Olao Magno, 1555), Sea Unicornu (Baffin, 1625), Le Licorne: Narwhal (La Peyrere, 1647), Monocerote (Albertus Magnus, 1651; Worm, 1655), Monoceros (Jonston, 1657), Zee-Eenhoorn (De Rochefort, 1662),

Fig. 5. The male narwhal according to Willughbi (1685) with the caudal fin on a broad vertical axis and pectoral fin in the shape of a bird's wing. Round eye, double blowhole. Left: the typical left maxillary tooth shown in its entirety. Top right, the clearly asymmetrical skull seen from above and below.

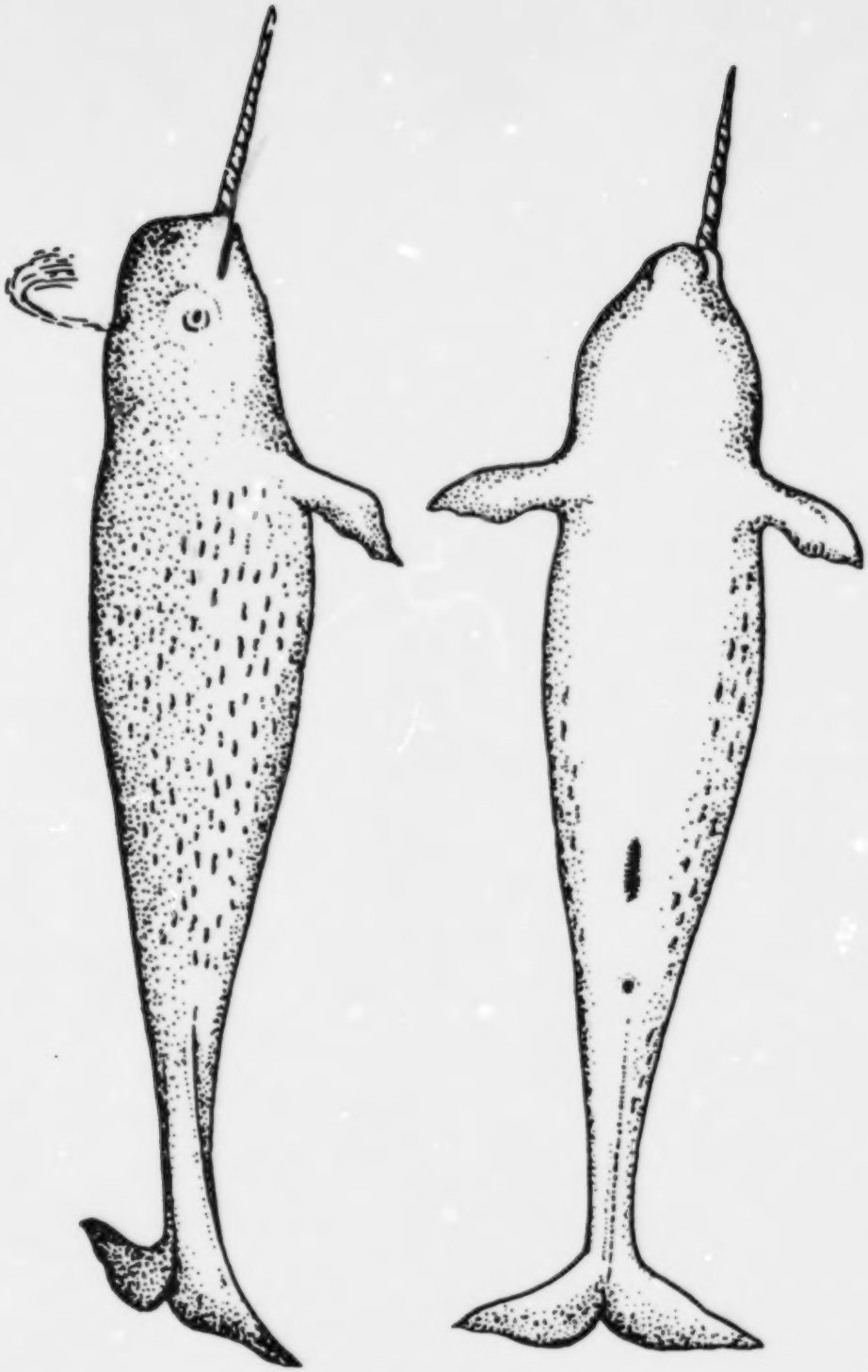

Fig. 6. The narwhal as shown by Fleming (1808). Left, lateral side; right, ventral side.

Unicornu marinum (Worm, 1655 and Tulpi, 1672), Einhorn: Monodon monoceros (Martens, 1675), Unicorn whale (Charlton, 1672), Unicornu groenlandico (Bartholin, 1678-1688), Narwhal (Grew, 1681), Monocerote pisce (Willugby, 1686), Monodon piscis (Ray, 1713), Eenhoorn (Zorgdrager, 1720), Meereinhorn (Langen, 1736), Narhual (Hampe, 1738), Unicorn Fish (Steigerthal, 1738), Ceratodon (Brisson, 1756), Eenhoorn-Visch (Houttuyn, 1762), Eenhoorn Fisch (Cranz, 1765), Eenhiorning, Narhval (Stauning, 1775), Licorne de Mer (Valmont de Bomare, 1775), Einhörn-Fisch (Fabricii, 1780), Narwhalus vulgaris (Lacédède, 1803), Ceratodon Monodon (Pallas, 1811), Narwali (Gérardin, 1817), Narwhalus (Desmarest, 1818), Ceratodon Monoceros (Ranzani, 1820).... Since Mulder (1835), the name Monodon monoceros is universally accepted and has been sanctioned by usage although it is actually a misnomer. The cephalic appendage of the narwhal is not a horn but a tooth consisting essentially of ivory. In addition, narwhal dentition comprises several teeth, not just the one tooth.

Some names, such as Diodon (Stoor, 1780), Oryx (Oken, 1815) and Tachynices (Brooks, 1828) were quickly abandoned.

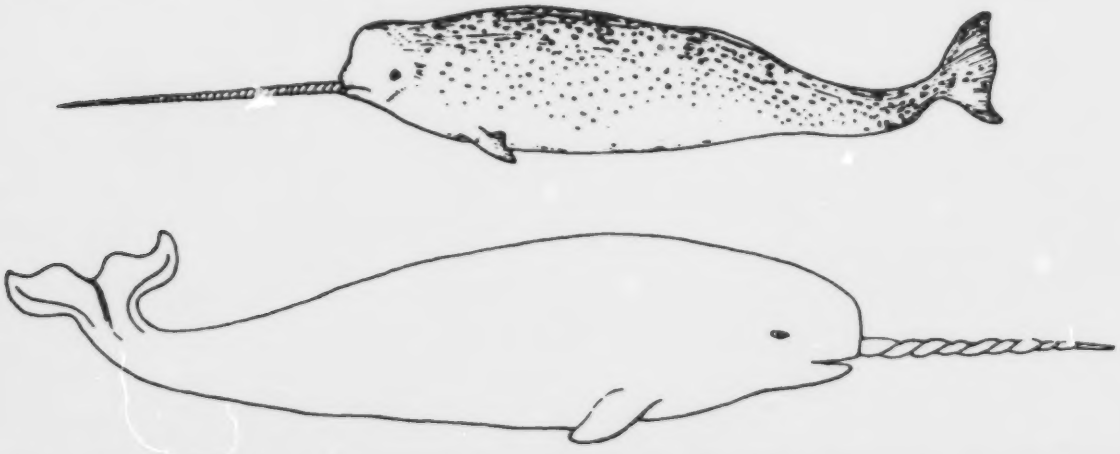

Fig. 7. Comparative morphology of the narwhal as depicted by Guérin (1837), top, and Kükenthal (1900), bottom, (in a male, 6 m long).

Our understanding of the narwhal has progressed very slowly and is still full of gaps. Whereas the anatomy of Phocoena and Tursiops had already been known for 150 years (Ray, 1671; Major, 1681; Tyson, 1681, etc.), Camper was pointing out in 1820 that the narwhal was one of the cetaceans about which we had "absolutely no anatomical observations." Fifteen years later, when Jules de Blosseville, the master of the ship "La Lilloise", disappeared during his Greenland expedition, the corvette "La Recherche" left Le Havre on May 1, 1825 under the direction of François Tréhouart. Orders were to look for traces of de Blosseville and to complete the unfulfilled mission. This expedition, like the one before it, had been prepared with the utmost care and the instructions Tréhouart received included zoological recommendations from Isidore Geoffroy Saint-Hilaire. At that time, the scientific community had only a narwhal skull with the maxillary tooth in its possession. It was therefore important to observe as many Arctic cetaceans as possible, collect specimens from all age groups and observe sizes and pigmentation in the living animal.

We now know that in addition to the giant tooth which is borne by the left maxilla and which, except in very rare instances, occurs exclusively in the male, pronounced sexual dimorphism also determines size. Present-day male narwhals have been known to be up to 4.70 m long, weighing as much as 1600 kg. The females are never more than 4 m long and weigh up to 900 kg (Mansfield et al., 1975). This said, a large female weighing 600 kg that died in Holland was found to be

4.20 m long (Van Deinse, 1931) and 6-m-long males have been seen.

1. THE NARWHAL SKIN

The narwhal has a typical cetacean skin. It is slightly keratinized. The epidermis is thin, whereas the dermis is very thick. The skin is remarkably smooth, firm and tough.

Pigmentation varies with age. In the foetus and newborn, the skin is basically blue with brownish variations or else, it is grayish in hue. Pigmentation is uniform throughout. As the animal grows older, the abdominal skin tends to become lighter, whereas on the back and flanks, a marble effect is produced by spots of different sizes, shapes and shades. They always appear darker against the background which is pale. Very old narwhals are yellowish white with gray spots on their backs. As a result, the Eskimos refer to these animals as "black fishes" to distinguish them from the "white fishes" or beluga whales.

There is no hair anywhere on the skin at any stage of development.

The head is equipped with a sort of fatty cushion that can be depressed to some degree. It consists primarily of fat tissue and, according to Fleming (1811), serves as a protective screen against sound.

The skin is smooth all over. A small ridge occurs on the back and, on the ventral side, another ridge extends from the anus to the tail. An umbilicus, urogenital opening and anus are found, in that order, along the medioventral line. The female has two paragenital mammary grooves (Fig. 8).

Since the phylogeny of cetaceans has not yet been elucidated, the cytological characteristics of the narwhal became of fundamental interest as the specific morphology of the animal had excluded it, along with the beluga, from the family Delphinidae. *In vitro* cultures ofperitoneal fibroblasts from a male specimen in a few days produced a sufficient number of cells undergoing metaphase for a chromosome count of 2n = 44 to be easily made and for the karyotype to be established. The chromosomes range in length from 8μ to 1.4 μ (the latter represent the Y chromosomes. The corresponding figure for the X chromosome is 4.4 μ) (Andrews et al., 1973). *Phocoenoides dalli*, *Tursiops truncatus* and *T.gilli*, *Globicephala scammoni* and *G. macrorhyncha*, *Stenella dubia*, *Delphinus delphis*, *Phocoena phocoena*, like *Eschrichtius* and *Balaenoptera* (*acutorostrata*, *borealis* and *physalus*) also have 2n = 44 chromosomes. Only *Physeter catodon* and *Kogia breviceps* have 2n = 42 chromosomes and their karyotypes differ from those of the above species (see Arnason, 1974).

2. THE NARWHAL HEAD

"Rostri apici propinqua longitudinalis. Caput maximum truncatum. Maxilla superior dentibus carens, inferior dentibus numerosis et symphisi longae, fere ad medium porrecta."

Lilljeborg, 1861

The narwhal head is blunt, almost round and remarkably small. It represents roughly one-seventh of the length of the body. The lower lip is fleshy and the upper lip protrudes over the lower lip. The mouth itself is small. "It is not more than the width of a man's hand" and is located on the underside of the head.

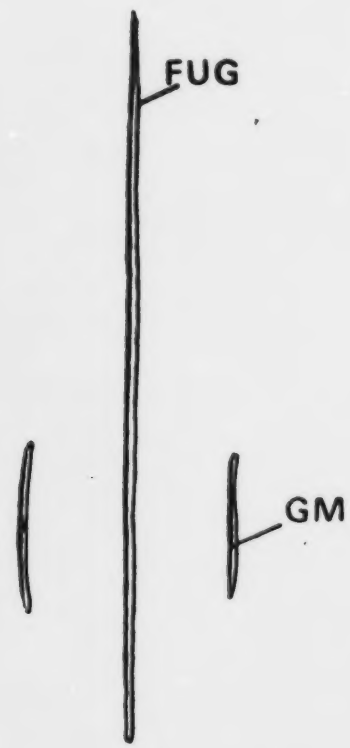

Fig. 8. The posterior ventral side of the female narwhal with the urogenital in the middle (FUG) and the mammary grooves on each side (GM)

See page 11 a.

Fig. 9. Longitudinal section of the rostrum and skull of a female narwhal (after Raven and Gregory, 1933). M = melon; S = spiracular sacs; E = blowhole; N = left bony naris; D = left maxillary tooth; Ma = left maxilla.

a. The Narwhal Melon

The rounded form of the adult head is produced by an accumulation of lipids ranging from 10 to 12 inches in length and 8 to 9 inches in height. The amount of oil lipids present in this cushion-like structure makes the forehead bulge to a variable degree with the result that the facial angle ranges from 60° to 90°, depending on the individual.

During the Greenland expedition of the American Museum in 1926, Raven had the opportunity of examining an adult narwhal. Serial parasagittal sections of a frozen head revealed a sort of oil-filled sac constituting the standard melon or spermaceti organ (Fig. 9). It was located under the thick fibrous skin above the bony rostrum and was surrounded by strong nasal muscles (some of which were transverse; the others, oblique). Contraction of these muscles forces the oil to the left and right bony narial tubes,

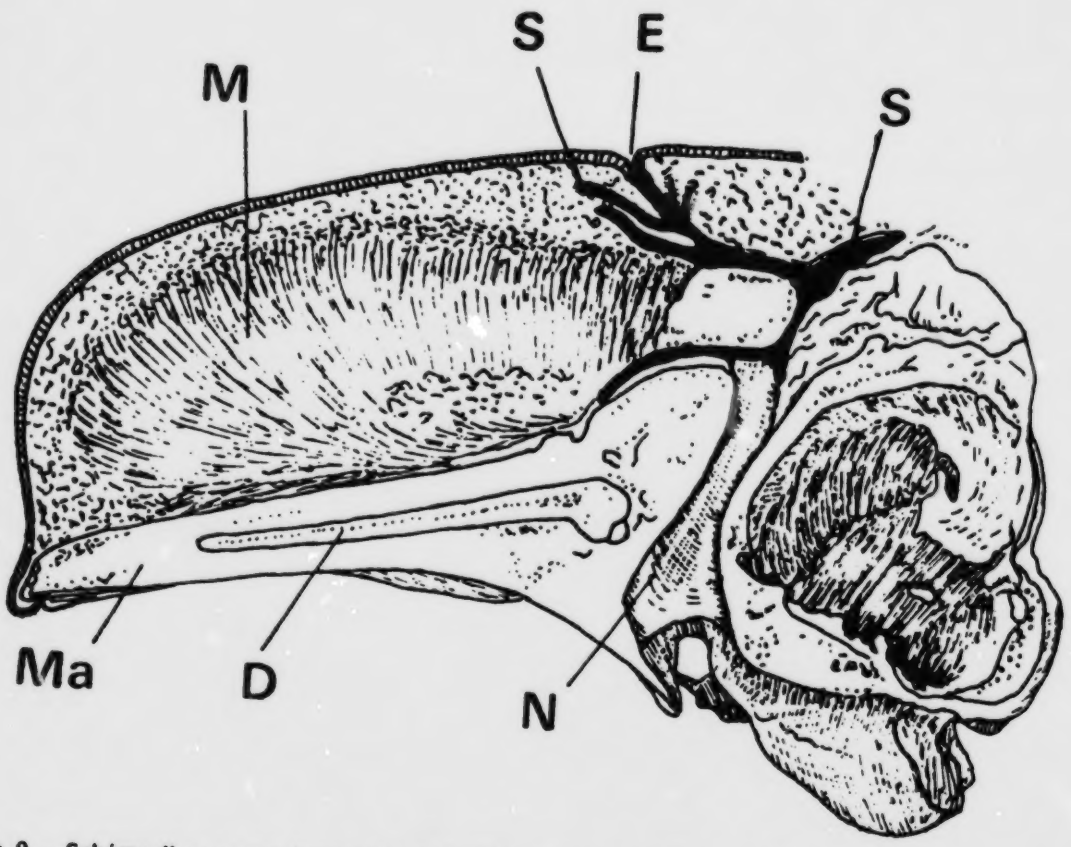

Fig. 9 — Schéma d'une coupe longitudinale du rostre et du crâne d'une ♀ de narval. (D'après Raven et Gregory, 1933). M : melon; S : sacs spiraculaires; E : évent; N : narine osseuse gauche; D : dent maxillaire gauche; Ma : maxillaire gauche.

Fig. 9. Longitudinal section of the rostrum and skull of a female narwhal (after Raven and Gregory, 1933). M = melon; S = spiracular sacs; E = blowhole; N = left bony naris; D = left maxillary tooth; Ma = left maxilla.

thereby blocking the spiracular sacs and the nasopharynx like two plugs. The larger of these plugs blocks the left narial bone and the smaller, the right narial bone whenever the narwhal sounds.

The nature of the lipids in the narwhal melon was elucidated by Robisch et al. (1972).

It is not known how the cetacean sonar system works. Certain hypotheses assigning an acoustical role to the melon have given rise to in-depth studies into the characteristics of the lipids in 15 odontocete (Arvy, 1977). In Monodon monoceros, melon oils differ radically from those in fat tissues taken from the posterior portion of the head. Lipids from the junction of the mandible with the bulla were found to contain 82.2 % triacylglycerols as compared to 85.5 % occurring in lipids from ordinary adipose tissue from behind the skull. This would suggest that the triacylglycerols are very similar and even identical, but qualitative analyses have shown that their components are radically different.

Melon lipids	Adipose tissue lipids
47.8 moles isovalerate	4.2 moles isovalerate
18.7 moles long-chain isoacids	0.9 moles long-chain isoacids
some acids that are monounsaturated at C_{16}-C_{18}	large numbers of acids that are monounsaturated at C_{14}-C_{16}-C_{18}- C_{20}-C_{22}
a few acids that are polyunsaturated at C_{16}	some acids that are polyunsaturated at C_{20} and C_{22}.

It was found that when the triacylglycerols in the melon contained 66 % of structures with 2 moles of isovalerate for 1 mole

of long-chain fatty acids, the ordinary fat tissue did not contain any di-isovaleroyl glycerides.

A corresponding similarity between the so-called "acoustic" tissues and ordinary fat tissue was reported in other previously examined odontocete, i.e., Delphinapterus leucas, Tursiops gilli, Phocoena phocoena. This led Robisch et al (1972) to conclude that the biosonar of marine cetaceans was a function of di-isovaleroyl glyceride compounds, irrespective of whether the animals inhabited warm or icy waters.

b. Narwhal Dentition

"The sea unicorn is a large fish which is found in large numbers in the glacial sea...this sea monster bears a heavy shiny white horn at the end of its nose. The horn forms a spiral like Saint-Denis in France."

Pomet, 1735

"The mouth of the narwhal is toothless, except for one modified incisor." *

Huber, 1934

The narwhal tooth was long mistakenly considered a horn. Olao Magno (1555), for instance, discussed the Unicorni africani, Unicornu borealis, etc. and Sachs (1676) in his Monocerologie distinguished between real and false unicorns.

Actually, the most extraordinary characteristic in the narwhal is its dentition. In the female, the teeth are not visible and remain embedded in the gums. In the male, on the other hand, dentition basically consists of a long maxillary tooth located on the left side.

* Anthropomorphically, the male's left tooth is occasionally referred to as an incisor or canine or tusk. Use of an incorrect term

Vestigial Dentition

The single long tooth borne by the left maxilla in the males of the species has been known for some time. It was not until 1835, however, that it was discovered (Mulder) that the animal had other, vestigial teeth. The latter were examined by a number of scientists: Wiegmann (1836), Rapp (1837), Van der Hoeven (1868), Turner (1872-1875), Gervais (1873), etc.

It was long held that the females did not have any teeth. The females were actually mistakenly identified as porpoises which whalers considered the females of the narwhal species. The female narwhal does have the same dental primordia as the male, but they do not develop.

Apparently, Mulder (1835) was responsible for discovering the second pair of teeth which remains vestigial. In 1872, Turner dissected a male narwhal foetus, 7¼ inches long, and found two dental papillae embedded in the gums in a dental sac on either side of the jaw. The anterior dental primordium was 5 mm from the tip of the maxilla and the second primordium was 2.5 mm behind the first. In 1875, Turner had the opportunity to dissect a second foetus, 5 feet, 5 inches long. The anterior extremity of the maxilla contained two aveoli which opened directly behind each other. The anterior alveolus contained a rudimentary cylindrical tooth, but the posterior sac enveloped an imperfectly developed tooth, 13 x 5 mm. Turner pointed out in 1912 that the adults, like the foetuses, had a pair of vestigial teeth behind the normally recognized pair.

---

cancels the original nature of this tooth.

In 1873, Gervais, who was not familiar with the work of his predecessors, examined a foetus, 115 cm long, and, in addition to the two teeth "corresponding to the known narwhal teeth" discovered "two other teeth, one on either side. These teeth were only a few millimeters long (8 x 3 mm) and located externally to the first two teeth. They were basically pyriform and the bulbs were already completely ossified. They were deciduous and would disappear at an early stage."

Fraser x-rayed foetal heads in 1932 and was thereby able to determine the sexually dimorphic characteristics of narwhal teeth (Fig. 10). Actually, it is not unusual for vestigial teeth to persist during adulthood. Not only are vestigial teeth found on one or both sides, but when they are absent, depressions of the same shape occur where these teeth should normally exist. This would suggest that they become dislodged as the skull develops anatomically.

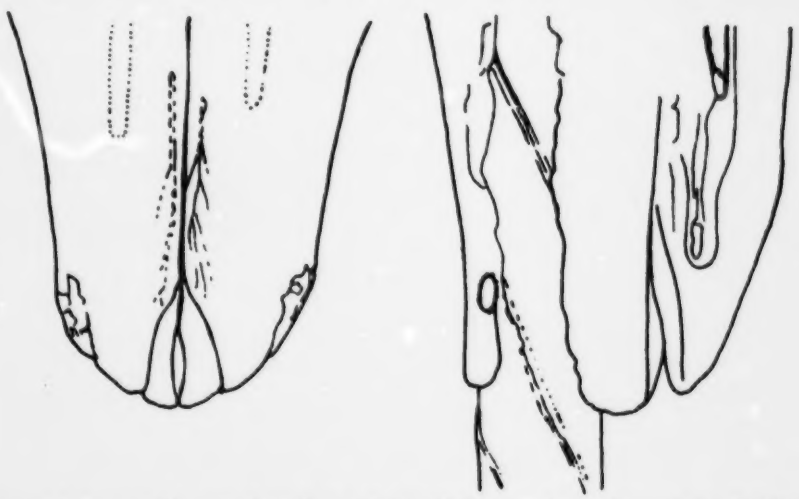

Fig. 10. Comparison of rostral extremities in the narwhal. Left, female. Right, male, ventral view (After Fraser, loc. cit.).

In a male foetus, 52 cm long, the teeth were 19 x 4.7 mm. The distal ends were rounded, the pulp cavities were wide open and the tips of the teeth touched the extremity of the rostrum exactly as in adult females (in adult males, the tip of the right tooth is located several centimeters behind the extremity of the rostrum). Next to these teeth, but peripheral to the latter, there were two vestigial teeth, 4.7 x 2.5 mm, one on either side of the maxilla (Fraser, 1938).

Permanent Dentition

"... That it is a sexual ornament employed in battle for the possession of the females there can be little doubt."

Millais, 1906

As early as the 12th century, the sea unicorn "horn" was a much-sought-after commodity. It was not until much later, however, that it was properly described, first by Tulpi (1641),then by Worm (1655). It is only then that its true narwhalian nature was established. All the early representations are inaccurate renditions of reality. Willughby's tooth (1685) is too wide for its length. The tooth portrayed in Tulpi's 1672 edition shows widely spaced equidistant striations from one end of the tooth to the other. Albers (1818), Mulder (1835), Vrolik (1849), Reinhardt (1862), Jäger (1851), and Clark (1871) observed that the skull was asymmetrical, particularly in the male. Albers (1818) was the first to establish the sexual dimorphism of the maxillary teeth. The female's two teeth are short and straight and equal in length. In the male, the right

tooth resembles the teeth in the female. The left tooth, however, grows at the same time as the individual, attaining maximum length in the adult. It is unusual for a male to have two long teeth (Bonnaterre, 1789; Brown, 1868) and more unusual still, to find a male-type long tooth in the female. The asymmetry of the skull cannot be attributed to the presence of a giant tooth on the left, as it is just as pronounced (see below) in the female bearing two intragingival teeth of equal length or in the male with two giant teeth.

In the male, roughly one-seventh of the tooth is embedded in the left dental alveolus. The free end is first twisted to some extent on its axis, the degree depending on the individual. A spiralling striation makes 5 or 6 turns around the shaft. In older males, the maxillary tooth has two spiralling grooves that lie next to each other. One is deep and wide, whereas the other is shallow. The tip of the tooth is always smooth and white and wedge-shaped, as if worn from use and rubbing. The base of the tooth is gray with often irregular incrustations.

At the end of growth, the left tooth in the male may be as much as 2.5 m long, while the right tooth barely exceeds 20 cm. In the female, the two teeth are as long as the right tooth in the male.

The two permanent teeth in the narwhal occur only in the maxilla. They do not originate between the maxillae and the intermaxillary

bone (G. Cuvier, dixit, 1823) nor in the intermaxillary bone (G. Cuvier, 1829 - F. Cuvier, 1836). They should not be mistaken for incisors or canines. They are distinct from all other mammalian teeth.

The literature contains numerous erroneous references* to "tusks" located on the right side in males. Scoresby (1820) and Reinhardt (1862), cetacean biologists and explorers, observed a large number of specimens and always found the giant maxillary tooth on the left side.

There is only one sure instance of a female narwhal with a male-type tooth. There could be no doubt in this case, for the animal was gravid, bearing two foetuses (Whatton, 1822).

It is not unusual for the left maxillary tooth in the male to break. Jurgensen, who methodically examined 314 males, found the teeth were broken at various points in 107 subjects. It should be mentioned here that the narwhal cannot swim backbards when it has passed through or under an obstacle. If the tooth has already been introduced into a passage, the animal uses it like a lever and breaks it. When a tooth has been sectioned, it bleeds profusely, releas- large amounts of dental pulp. Characteristically, it heals rapidly and grows within a short time.

The fresh male tooth is fairly brittle and can break like glass. When detached, it becomes dehydrated and shrinks in size so

* In: G. . Cuvier, F. Cuvier, Lacépède, Meckel, Rapp, Lilljeborg, Owen, Pander and d'Alton, Fabricius.

that it can lose 16 % of its weight in a single summer. It then becomes much more break-resistant (Degerbøl and Freuchen, 1935).

Male narwhals do not use their teeth to attack one another or any other adversary, for that matter. The narwhal does not defend itself from attackers. It flees. Even when caught in the ice and competing with other individuals for air, it will not use its tooth as a weapon. It does not seize its prey by impaling it , as suggested by Scoresby. In all likelihood, impalement, should it happen, is an accidental occurrence.

This long tooth does not make it any easier for the male to feed. Boitard (1846) claimed that the male of the species used its tooth to detach oysters and other mollusks from rocks and the rocky sea floor, but females which are not equipped in this manner are able to feed just as well as the males.

This enormous tooth might even be a hindrance for the males. A tooth, 1.64 m long, was found to weigh 2.75 kg. Two teeth, each 2.30 m in length, weighed 6.20 kg and 7.40 kg, respectively. The biggest tooth on record was collected at the time of Vanhöffen (1897) and found to be 22.5 cm in circumference at the base. When an adult male skull is 57.5 cm long and the left tooth, 1.785 m long (Millais, 1906), we can rightly say that it takes a narwhal to put up with such an appendage.

Comments

Over the past twenty years, odontocete teeth have been used to estimate the age of the animals. This is done by counting the number of superposed dentine lamellae. This technique has been used in Prodelphinus caeruleoalba (Nishiwaki and Yagi, 1953), Tursiops truncatus and Globicephala melaena (Sergeant, 1959 and 1973), Delphinus delphis (Kleinenberg and Klevezal, 1962), Physeter (Boschma, 1951; Ohsumi et al, 1963; Best, 1970; Gambell, 1972), Stenella caeruleoalba (Kasuya, 1972), Hyperoodon ampullatus (Benjaminsen, 1972 and Christensen, 1973), Stenella attenuata (Kasuya, 1976 and Perrin et al, 1976), Berardius bairdii (Kasuya, 1977) and even in Delphinapterus leucas (Brodie, 1960-1969-1971 and Sergeant, 1963). The latter species closely resembles the narwhal in its general morphology and cold-water biotope. In spite of this, narwhal age has not yet been estimated by means of tooth length and dentine lamellation.

c. The Narwhal Skull

The narwhal skull is relatively small and remarkably wide and short. Observers have all commented on its asymmetry (Clark, 1871; Kükenthal, 1908; Nass, 1967...). The skull is flat, concave on top with a flattened wedge-shaped protuberance towards the front end. It is this protuberance that lodges the base of the giant tooth. Above this strictly dental protuberance is located the oily melon cushion (10 to 12 inches long and 8 to 9 inches high, Scoresby, 1822). The cushion gives the narwhal head its rounded appearance. It may

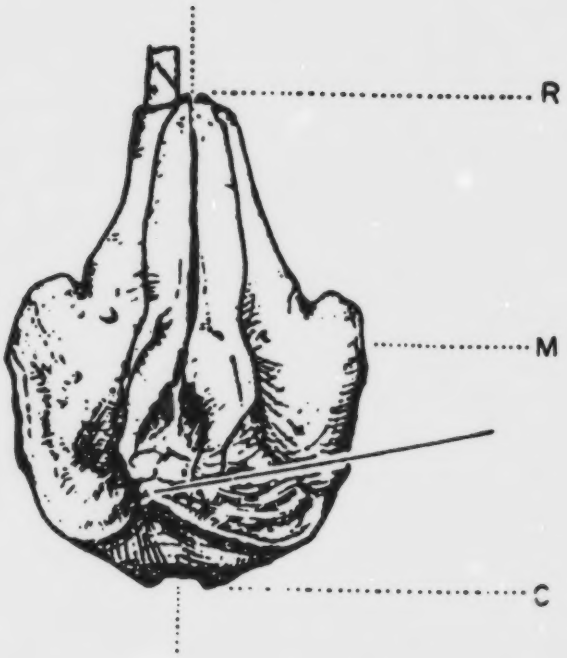

Fig. 11

Asymétrie du crâne de narval, d'après les mensurations faites sur 20 crânes, par Ness (1967). La longueur moyenne du crâne, RC est de 49,36 cm (les longueurs extrêmes étant 14,6 et 60,2 cm); l'axe longitudinal est dévié de + 32,7, l'axe M étant dévié de + 3,4. La torsion du crâne augmente à mesure que le narval grandit; l'asymétrie est la même que les narvals soient pourvus de dent maxillaire géante, unique ou double, ou qu'ils n'aient pas de dent géante.

Fig. 11. Asymmetry of the narwhal skull based on measurements of 20 skulls taken by Ness (1967). The mean length of the skull, RC, is 49.36 cm (values range from 14.6 cm to 60.2 cm). The longitudinal axis deviates by +32.7 and the M axis by +3.4. Torsion of the skull increases as the animal grows. Asymmetry is the same whether the animal lacks giant teeth or is equipped with one or two.

See page 20 a.

Fig. 11. Asymmetry of the narwhal skull based on measurements of 20 skulls taken by Ness (1967). The mean length of the skull, RC, is 49.36 cm (values range from 14.6 cm to 60.2 cm). The longitudinal axis deviates by +32.7 and the M axis by +3.4. Torsion of the skull increases as the animal grows. Asymmetry is the same whether the animal lacks giant teeth or is equipped with one or two.

vary in size causing the forehead to bulge to a corresponding degree. The facial angle ranges from 60^{o} to 90^{o}.

Tomilin (1967) showed that in this large skull, the pterygoid muscles are separated from each other by the base of the vomer and the palatine bones (Fig. 12). Numerous measurements have revealed the differences that existed between skull bone pairs (Table)

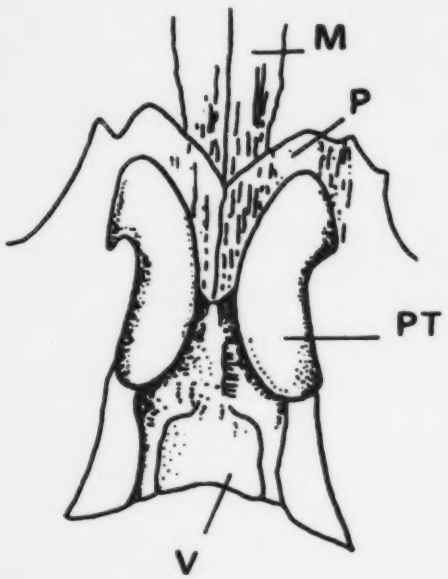

Fig. 12. Diagram of bones at the base of the narwhal skull (After Tomilin, 1967). M = maxilla; P = palatine bone; PT = pterygoid muscle; V = vomer. No significant dissymmetry is shown.

Table

Mean Measurements in cm of Cranial Bones in Narwhal Skeletons, 3.90 m to 4.52 m long (mean length: 4.21 m. (After Tomilin, 1967)

length of basal condyle	61.3	length of palatum osseum	37.4
length of zygomatic bone	39.7	tip of rostrum to bony naris	42.6
supraorbital width	36.5	pterygoid fossa	12.9
condyle width	15	height of left occipital condyle	7.6
rostrum length	28.8	width of right occipital condyle	5.3
rostrum width at base	21.7	width and height of occipital foramen	5 x 4.9
mid-rostrum width	15.7	mandible length	50.5
length of temporal fossa	13	length of mandibular dental canal	19.25
width of left temporal fossa	6.25	vertical diameter of the dental alveolus at the anterior extremity of the mandible	5.75
width of right temporal fossa	5.25	horizontal diameter of this alveolus	5.9
maxilla length	55.3		
length of left premaxilla	42.9		
length of right premaxilla	44.8		

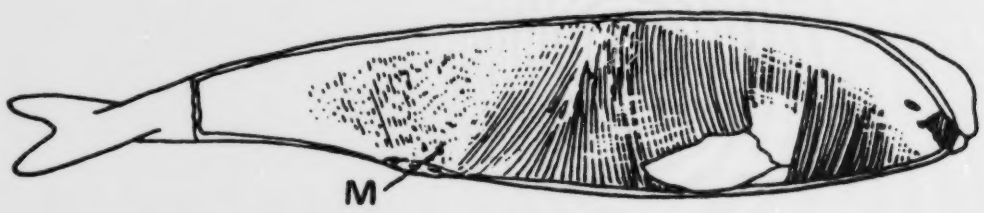

Fig. 13. Panniculus carnosus and sphincter colli in a narwhal foetus, 1.563 m long (after Howell, 1930). M indicates the position of the mammary excretory orifice.

Cranial dissymmetry may be clearly seen in the temporal fossae and premaxillary bones.

The narval mandible is blunt toward the front and strongly fused (Van Beneden and Gervais, 1880).

d. Facial Muscles in the Narwhal

The facial musculature has been closely examined in only one foetal specimen.

At term, the narwhal foetus differs radically from all other mammal and even cetacean foetuses.

All the facial muscles in the narwhal are dissociated by oily sinuses of all sizes that are interspersed with special vein spaces. The latter assume a cavernous appearance around the eye and ear systems. In addition, there are numerous dense muscle bundles at the muffle. These radiate through the subcutaneous tissue and insert upon the dorsal cephalic skin. A system of this type apparently does not exist in any other aquatic mammal. Innervation remains the best guide for dissection.

Asymmetry in the muscle system parallels that observed in the bones. On the right, the sphincter colli primitivus disappears into the panniculus carnosus which is extended anteriorly as well as posteriorly by aponeuroses. The post-auricular occipital muscle

group is larger on the left side than on the right. These muscles insert upon the eustachian tubes which are very small.

A sphincter colli profundus is continuous with the sphincter colli primitivus. The pars auris is formed primarily by a tendon plate which is attached to the vestigeal external ear. The pars auris is continuous with the pars pre-auricularis. The pars palpebralis and pars oris form a continuous sheet which is more developed in the area of the pars oris. A deep muscle layer lines the mouth opening and is comparable to a very simple buccinator muscle. The vestibulum oris consists of a small double-branched diverticulum. The lower of the two branches extends over a short distance at a lateral angle to the mouth. The upper branch connects with the bony palate.

There is a small auriculolabial tendon plate which widens toward the front into a muscle strip. The latter passes beneath the musculus orbicularis oculi, dips under the pars palprebralis of the sphincter colli profundus and ends a short distance from the mouth.

The mucculus orbicularis oculi is well developed and actually forms a sphincter around the eye.

The muscles of the blowhole insert upon the frontal, premaxillary and maxillary bones. These muscles form complexes that may be characterized as pars labialis, pars nasalis and maxillonaso-

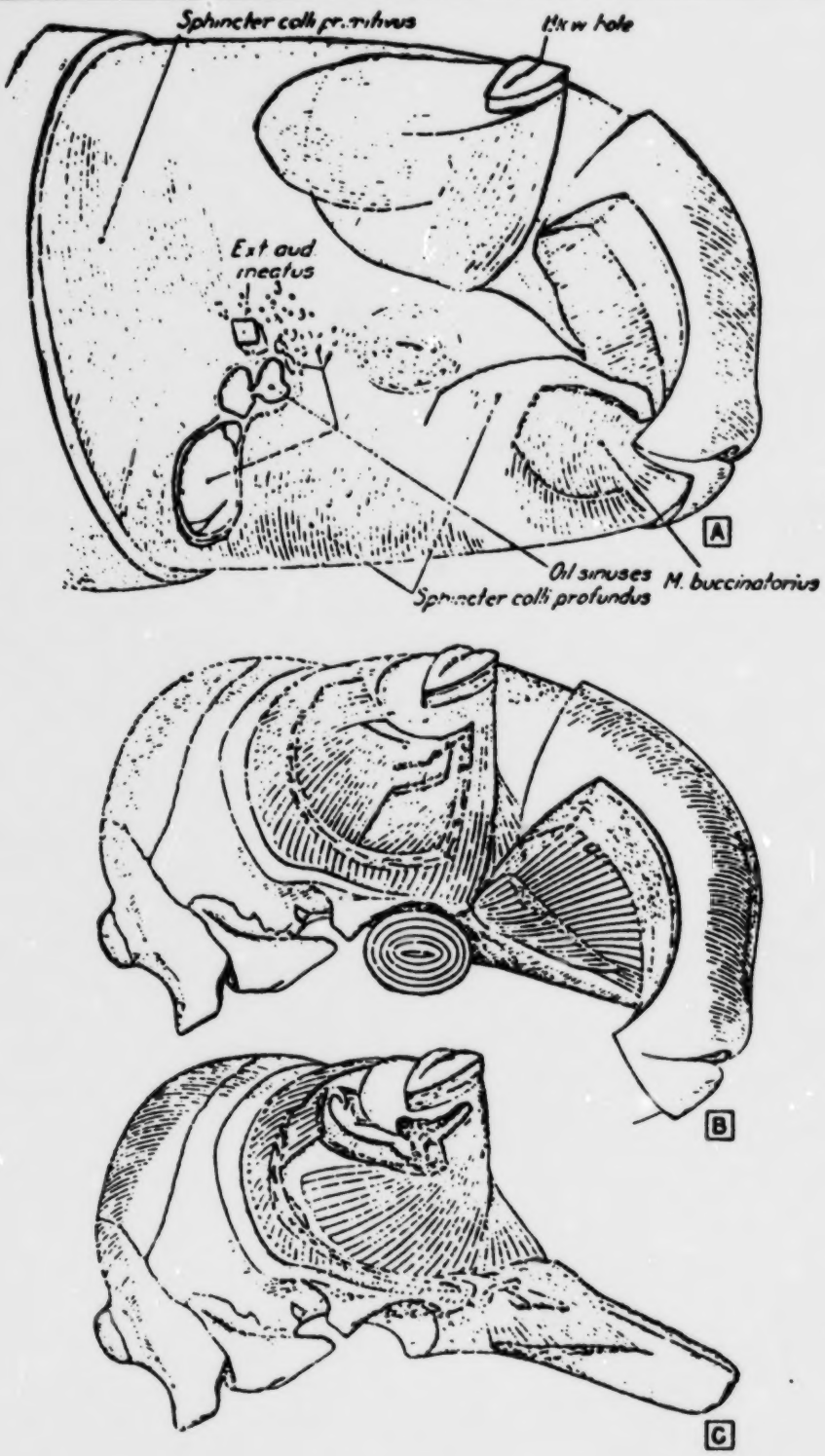

Fig. 14. Superficial fachial muscles in the narwhal (A) and underlying muscles (B and C). After Huber, 1934.

labialis.

Once the facial nerve emerges from the facial foramen in the mastoid region, it supplies a few minute fibers to the rudimentary ear muscles, the sphincter colli profundis and the musculus orbicularis oculi. It curves around the pre-orbital apophysis of the maxilla, then just before the orbit, divides into a number of branches. It subsequently curves upward, then downward to divide still further and supply branches to the blowhole muscles. Two terminal branches curve medially toward the front to innervate the anterior blowhole muscles and the muscles at the rostrum base. The latter muscles include bundles that penetrate or surround the melon (Fig. 15).

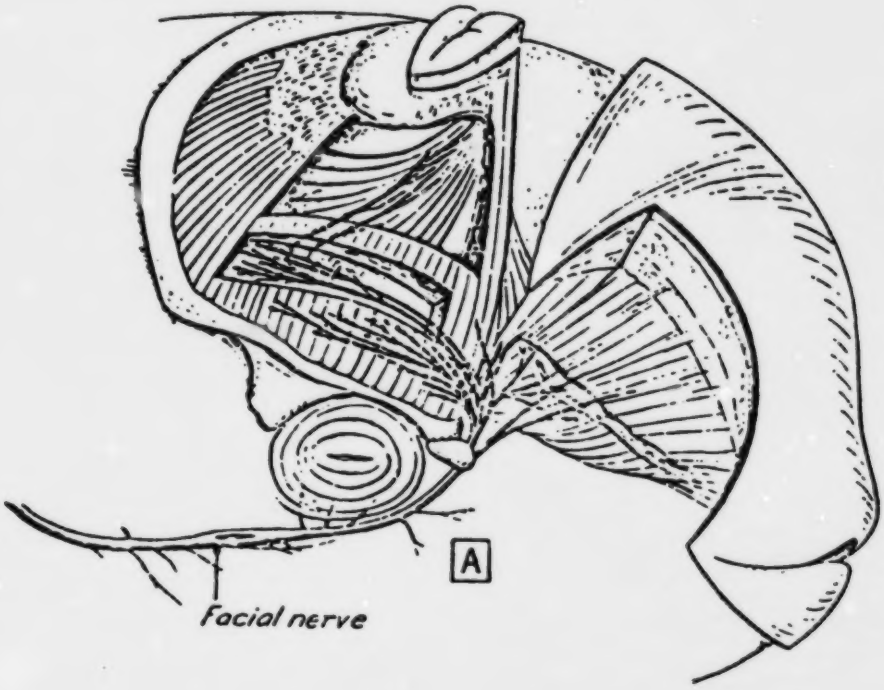

Fig. 15. The facial nerve and its branches in the narwhal. After Huber, 1934.

e. The Narwhal Blowhole

The blowhole is situated at the top of the head, at the same level as the eyes or else, slightly behind them. It is 6 to 8 cm long and faintly crescent-shaped. The first naturalists, Bonnaterre (1789), Gérardin (1817) and Guérin (1837), described a fringed comb-like rim. In fact, the latter is smooth and regular.

The blowhole cavity, or spiracular cavity, contains a remarkably extensive system of diverticula. Three pairs of large nasal sacs communicate with the blowhole. There is also a pair of small lateral recesses (Fig. 9). Consequently, it is possible to distinguish an anterior premaxillary pair, a posterior nasofrontal pair, and an anterolateral pair of sacs which in back communicate with the naso-frontal sacs. In front, they lie side by side on the median plane. The lateral recesses of the blowhole are cup-shaped (Huber, 1934). The asymmetrical structure of the blowhole sacs has not been studied in detail.(Fig. 16).

See Page 27 (a)

Fig. 16. Blowhole system in the narwhal. A. with the surface tissues cut away and folded back. B. after dissection. C. after reconstruction of the spiracle and associated diverticula (After Huber, 1934).

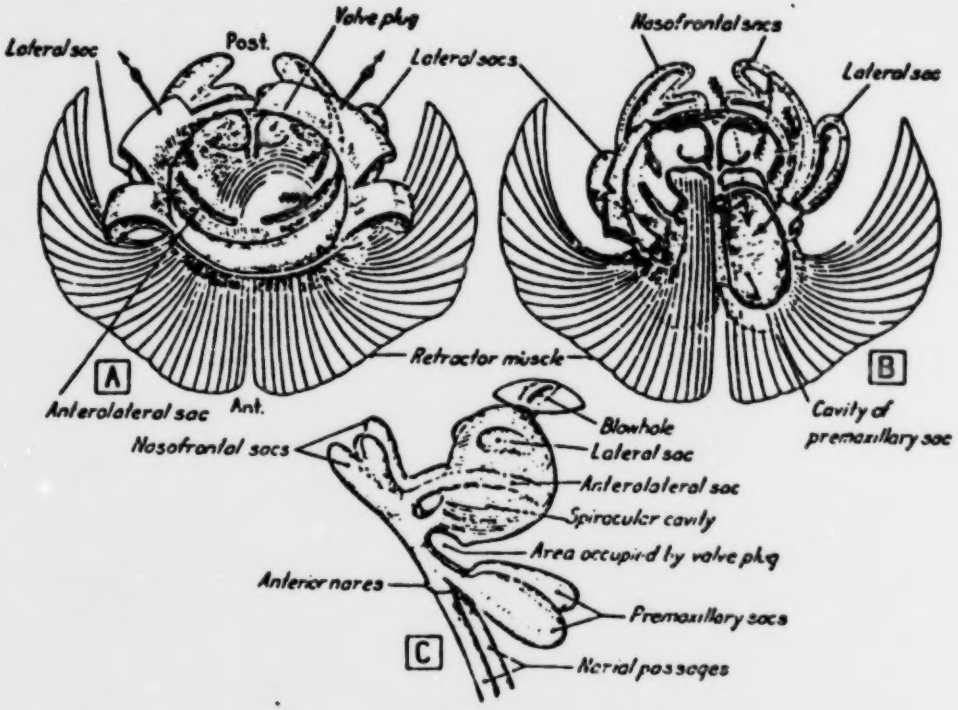

Fig. 16 — Schéma de l'appareil de l'évent, chez le narval. En *A* : avec sa surface découpée et rabattue; en *B* : après dissection; en *C* : après reconstruction du spiracle et des diverticules qui lui sont associés. (D'après Huber, 1934).

Fig. 16. Blowhole system in the narwhal. A. with the surface tissues cut away and folded back. B. after dissection. C. after reconstruction of the spiracle and associated diverticula (After Huber, 1934).

f. The Narwhal Ear

Like all cetaceans, the narwhal has no external ear. There is a minute closed pore behind the eye (Fig. 17). The ear ossicles are ankylosed. We owe our understanding of the inner ear to Kellogg (1928) and Eales (1950). The latter made a wax reconstruction of the membranous labyrinth and the ossicles in a foetus (Fig. 19 a and b). The bulla is relatively large and probably involved in conducting sound waves through the head bones and brain. Tiny facial muscles insert onto membranous and cartilaginous components of the inner ear.

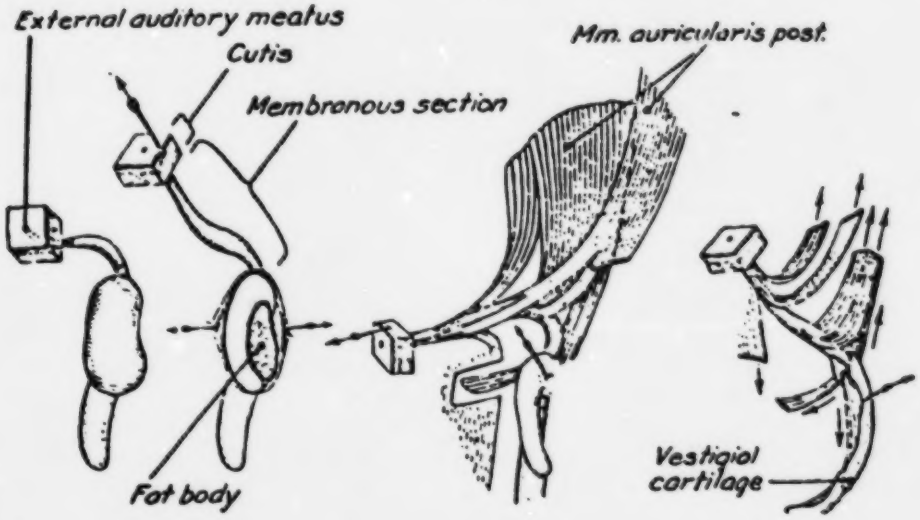

Fig. 17. Extra-cranial components of the auditory system in the narwhal. (After Huber, 1934).

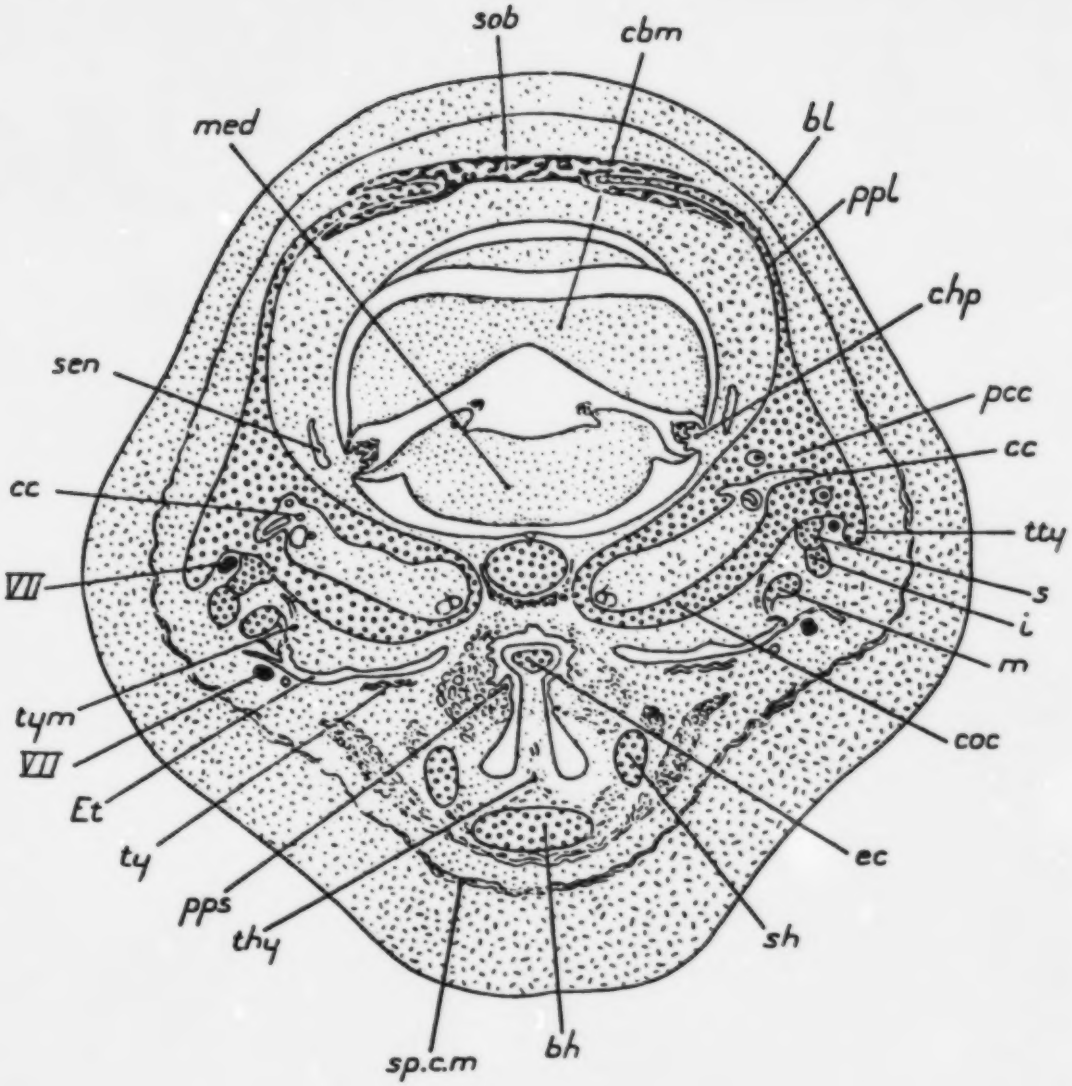

Fig. 18. Cross section of a foetal head through the canicular and cochlear segments of the auditory capsule, the auditory ossicles and the intranarial epiglottis (After Eales, 1950).

sob = supraoccipital bone
med = medulla oblongata
sen = saccus endolymphaticus
cc = canicular segment
VII = facial nerve
tym = tympanic membrane
Et = eustachian tube
ty = tympanic bone
pps = palatopharyngeal sphincter
thy = thyrohyoid muscle
spcm = sphincter colli
bh = basihyal bone

cbm = cerebellum
bl = subcutaneous adipose tissue
ppl = parietal bone
chp = choroid plexus
ppc = parietocapsular commissure
tty = tegmen tympani
s = stapes
i = incus
m = malleus
coc = cochlear segment
ec = epiglottic cartilage
sh = stylohyoid cartilage

g. The Eyelids and Eyes in the Narwhal

The eyes are behind and slightly above the mouth, 30 to 35 cm from the tip of the muffle. The pupils are black, the irises, chestnut brown. The sclera is white (Gray, 1866, dixit), but no one knows if all narwhals have the same colour eyes.

The surface of the skin surrounding the eyes is horny, stiff and non-retractile, suggesting that the eyes are permanently exposed to the water. Actually, an epidermal stratum under the surface tegument is differentiated into lids that close by contraction of orbicular muscles of the eyes. (Fig. 20).

The adult eye is roughly one inch in diameter (Thorburn, 1921).

3. THE BODY AND TAIL IN THE NARWHAL

The body is spindle-shaped and can attain a length of 16 feet. The head is not clearly set off from the body. The back is slightly convex. Instead of the standard dorsal hump or fin, there is a low, 5-cm-high ridge, 75 cm long in the adult male.

As in all cetaceans, the tail is situated on a broad horizontal axis. According to Jardine (1837), it is 20 inches long and 4 feet wide. Thorburn (1921) reported it could range in length from 15 to 20 inches and in width from 3 to 4 feet.

(1) Bone Structure

a) The Thorax

The thorax consists of cervical and dorsal vertebrae, and 12

ribs, 6 of which are floating and 6, attached to the sternum which has been variously described by different authors. Like all cetaceans, the narwhal does not have a clavicle.

According to Scoresby (1822), the sternum resembles an elongated heart with the narrower portion at the anterior end. Tomilin (1967) described the sternum as bipartite with 3 or 4 joints.(Fig. 21). He found the structure varied greatly in adults. The posterior end he described was also very different from that observed by Anthony (1898) and the sternum of the specimen on display at the Paris Museum of Natural History (Fig. 22) (Arvy and Pilleri, 1977). In the latter case (Fig. 23), the sternum is trapezoidal with a large anterior base and a faint depression in the middle. It consists of a single piece, 39 cm long and 29 cm wide in front and 9 cm wide in back. Two symmetrical appendages, 5 cm long, fused at the median line over a distance of 4 cm, extend the sternum. The male sternum shown in Fig. 24 is essentially the same. In the foetus, the sternum comprises 6 elements joined by a long longitudinal sulcus and two transverse sulci. Except for the sternal perforations seen in Fig. 23 and Fig. 23 a, there are no traces of these sulci in the adult. Such morphological differences in the sternum justify research based on the age, sex and geographic origin of the animals.

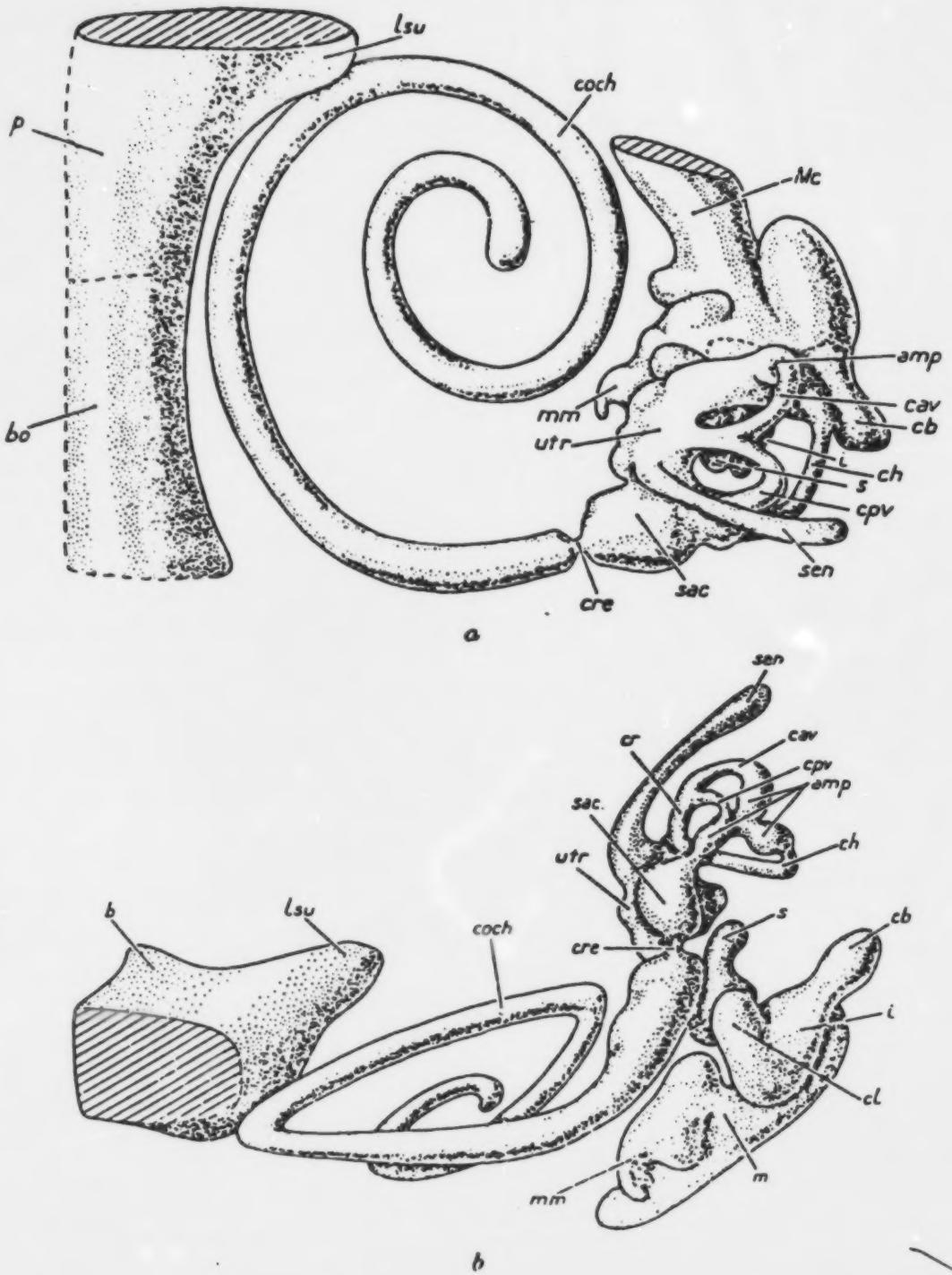
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Fig. 19

See page 32

Fig. 19. Reconstruction, from serial sections, of the membranous labyrinth and auditory ossicles in a foetus (After Eales, 1930). a = dorsal view showing the relative sizes of the canicular and cochlear segments of the labyrinth. b = posterior view of the ossicles.

p = basal or parachordal plate
bo = basioccipital bone
lsu = lamina supracochlearis
coch = cochlear segment
Mc = Meckel's cartilage
mm = manubrium of malleus
utr = utricle
amp = ampulla
cav = vertical anterior semicircular canal
cb = crus breve of incus
i = incus
ch = horizontal semicircular canal
s = stapes
cpy = vertical posterior semicircular canal
sen = endolymphatic sac
sac = saccule
cre = canalis reuniens between the saccule and cochlea
a = auditory capsule
b = mouth cavity
m = malleus
cl = crus longum of incus

Fig. 20. Diagram of system for closing the eyelids (After Huber, 1934)

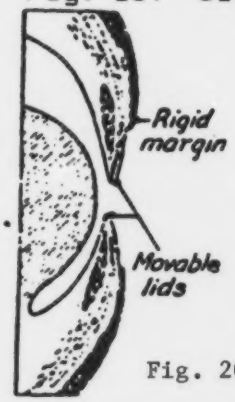

Fig. 20

Fig. 21. Two male sternums, seen by Tomilin, 1967

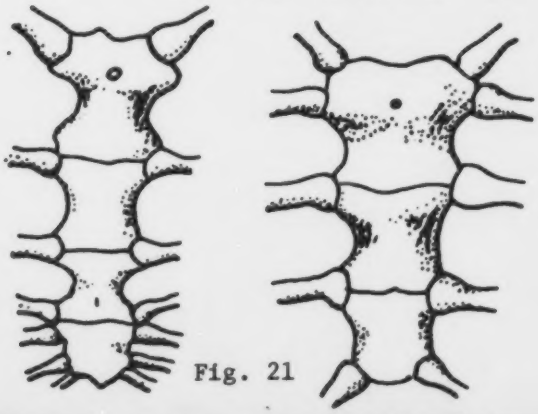

Fig. 21

Fig. 22. Posterior extremity of the narwhal sternum, seen by Anthony, 1898.

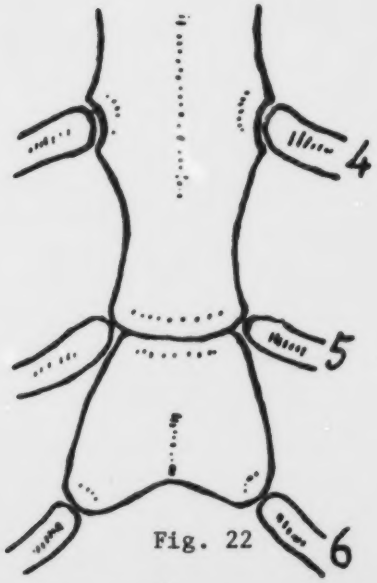

Fig. 22

Fig. 23 — Vue dorsale du sternum du narval ♂ exposé dans la galerie d'anatomie comparée du Musée d'histoire naturelle de Paris. L'apophyse latérale, comprise entre la première et la deuxième côte, sur la face ventrale du sternum apparaît nettement, à gauche (Photographie de Mr. Gordon, du MHN de Paris).

Fig. 23. Dorsal view of the sternum of a male narwhal on display in the comparative anatomy gallery of the Museum of Natural History in Paris. The lateral apophysis between the first and second ribs on the ventral side of the sternum may be clearly seen at the left (photograph by Mr. Gordon, Paris MNH).

Fig. 23 a. Sternum of a male narwhal at the Museum of the Royal Institute of Natural Sciences in Brussels (photography obtained through the courtesy of Mr. De Smet).

See page 35 a.

Fig. 24. Photograph of a female narwhal sternum. Ventral side, left. Dorsal side, right. The sternum entered the collection of the Paris Museum of Natural History in 1869. It is essentially trapezoidal with a large anterior base. It provides insertion for 6 ribs. Note the prominent lateral apophyses above the sites of insertion of the second ribs (photograph by Mr. Gordon, MNH, Laboratory of Comparative Anatomy).

The dorsal side of the thorax is lined laterally by relatively small scapulae with distinct acromial and coracoid processes (Fig. 25).

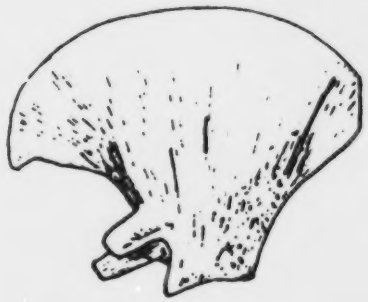

Fig. 25 — Schéma de l'omoplate du narval, vu par Tomilin (1967), avec son acromion et sa coracoïde bien développés.

Fig. 25. Narwhal scapula, seen by Tomilin (1967) with well-developed acromion and coracoid processes.

Fig. 24 — Photographie du sternum d'un narval ♀, face ventrale à gauche, face dorsale à droite, entré au Musée d'Histoire naturelle de Paris en 1869; trapézoïde à grande base antérieure, donnant insertion à six côtes, le sternum est en outre remarquable par l'apophyse latérale puissante, qui surplombe l'insertion de la deuxième côte. (Photographie de Mr. Gordon, du MHN, Laboratoire d'Anatomie comparée).

Fig. 24. Photograph of a female narwhal sternum. Ventral side, left. Dorsal side, right. The sternum entered the collection of the Paris Museum of Natural History in 1869. It is essentially trapezoidal with a large anterior base. It provides insertion for 6 ribs. Note the prominent lateral apophyses above the sites of insertion of the second ribs (photograph by Mr. Gordon, MNH, Laboratory of Comparative Anatomy).

b) The Spinal Column

The spinal column extends over six-sevenths of the body. The vertebral formula comprises 50 to 56 vertebrae, depending on the observer:

Gray (1871): 7 C + 11 D + 8 lumbosacral + 24 caudal = 50.

Lilljeborg (1861): 7 C + 12 D + 9 lumbosacral + 25 caudal = 53.

Scoresby (1822): 7 C + 12 D + 35 lumbococcygeal = 54, 12 of which extend in the tail to within one inch of the tip.

Tomilin (1967): 7 C + 11 to 12 D + 6 to 10 L + 26 to 27 caudal = 50 to 55.

The spinous processes shorten towards the 15 lumbar vertebra and are barely perceptible at the 19th. The abdominal processes begin between the 30th and 31st vertebrae and disappear between the 42nd and 43rd (Scoresby, 1822).

The spinal cord terminates at about the 40th vertebra (Scoresby, 1822).

c) The Abdomen

"The right and left pelvic bones are slightly asymmetrical in size and situated just below the first and second caudal and the last lumbar vertebra."

Tomilin, 1967

The two paramedian abdominal parietal bones usually escape notice in the narwhal. Howell (1930) figured them in his narwhal foetus, 1.563 m long. They resemble small sticks (Fig. 26).

Fig. 26 Schéma de la musculature profonde chez un fœtus de narval de 1,563 m de long. (D'après Howell, 1930) OA = os abdominal; PP = muscle pectoral profond; FG = fente génitale; GD = grand droit abdominal; SC = sterno-costal; SM = sterno-mastoïdien

Fig. 26. Deep muscle structure in a narwhal foetus, 1.563 m long (After Howell, 1930). OA = abdominal bone; PP = deep pectoral muscle; FG = genital cleft; GD = great right abdominal muscle; SC = sternocostal muscle; SM = sterno-mastoid muscle.

These two bones were not observed by Clark (1871) although he examined his specimen with great care. His failure to find them may have been because he was looking for these so-called "pelvic" bones in the vicinity of the spinal column.

d) The Pectoral Flippers

The pectoral flippers are short. In the adult, they are 30 to 40 cm long, i.e., roughly one-fourth to one-tenth the length of the body. In a male, 3.79 m long, they were situated 77 cm behind the tip of the muffle and were 38 x 19 cm long (Fleming, 1811).

The scapulae do not exhibit any characteristics that are peculiar to the narwhal. They are like those found in other odontocete (Fig. 27) but have relatively large coracoid and acromial processes (Gray, 1871).

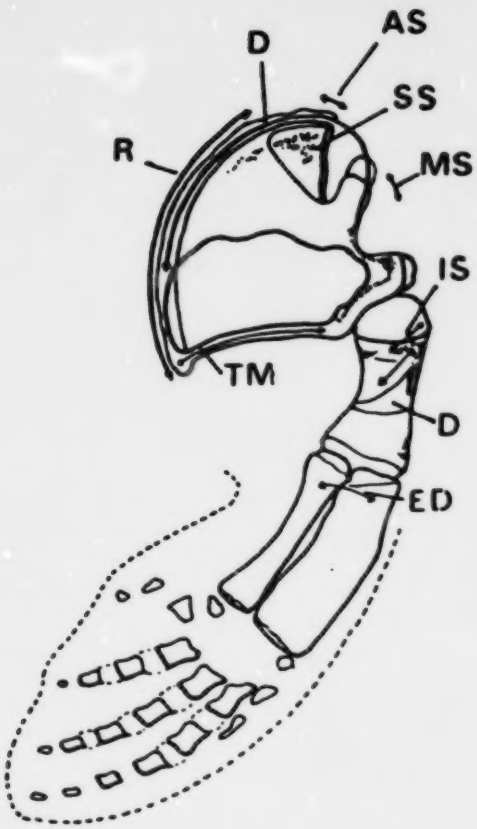

Fig. 27 – Insertions musculaires sur les os de la nageoire pectorale, chez un fœtus de narval de 1.563 m, d'après Howell (1930). R : muscle rhomboïdal; D : deltoïde; AS : atlanto-scapulaire; SS : supraspinal; MS : masto-scapulaire; IS : infraspinal. ED : extenseur des doigts; TM : *teres major*.

Fig. 27. Insertions of the muscles on the pectoral flipper in a narwhal foetus, 1.563 m long (After Howell, 1930). R = rhomboid muscle; D = deltoid muscle; AS = atlantoscapular muscle; SS = supraspinous muscle; MS = mastoscapular muscle; IS = infraspinous muscle; ED = extensor muscles of fingers; TM = teres major muscle.

The humerus has a large, rough, highly developed tuberosity and, toward the middle of the internal side, there is a rough elevation (Fig. 28). The radius and cubitus are short and flat with blunt margins. The radius bears a fairly pronounced elevation on its anterior border at the site where the anterior third meets with the posterior two-thirds. The radial and ulnar bones are small; the intermediate bone is relatively large (Bambeke, 1866). The fifth finger is twisted so far to the back that it virtually forms a right angle with the cubitus (Fig. 29). Narwhal metacarpals are epiphyseal. Depending on the authors and subjects, there are 14 to 30 phalanges. Actually, the number varies considerably with age.

Variation in the Number of Phalanges

1) Foetus

According to Leboucq (1889), who based his observations on three foetal specimens, the number of phalanges decreases from 25 to 21 as the hand increases in size:

Hand, 5 mm long:

I	II	III	IV	V	
2	8	6	5	4	= 25

Hand, 9.6 mm long:

2	8	6	5	3	= 24

Hand, 15 mm long:

2	7	5	4	3	= 21

For Kükenthal (1889):

Foetus, 13.8 cm long:

2	9	8	6	5	= 30

Foetus, 29 cm long:

2	8	7	5	4	= 26

For Howell (1930):

Foetus, 1.563 m long:

2	6	5	4	3	= 20

2) Adults:

For Van Beneden and Gervais (1880):

2	5	4	2	2	= 15

For Tomilin (1967):

1-2	5-8	4-6	2-4	2-3	= 14-23

In conclusion, the number of phalanges decreases as the foetus grows. In addition, the distal phalanges are relatively longer in smaller foetal specimens than in larger ones. They account for 22.14 % of the total length of the fingers in a very young foetus, but for only 12.46 % in a foetus with hands three times as big, i.e., 15 mm compared to 5 mm (Leboucq, 1889).

e) The Tail

The tail lacks any bone structure other than the terminal vertebrae. Some authors refer to the latter as caudal, others as coccygeal vertebrae. The 12 distal vertebrae extend for a considerable distance along the axis of the tail, somewhat like in the Delphinus delphis foetus (Arvy, 1977. Pl I, Fig. 1) to roughly within one inch of the extremity of the tail (Scoresby, 1822). The remainder of the tail consists of fibromuscular tissue.

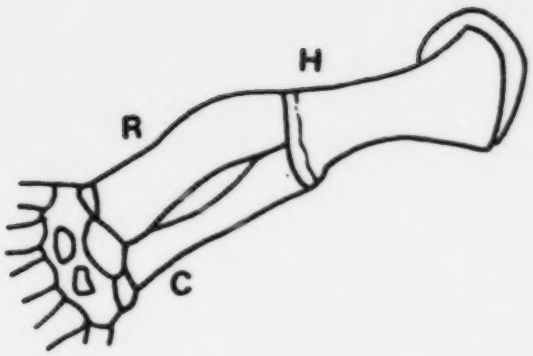

Fig. 28 — Les os de la nageoire pectorale de *Monodon monoceros*, d'après Van Bambeke (1866); H : humérus; R : radius; C : cubitus.

Fig. 28. Pectoral flipper bones in Monodon monoceros (After Van Bambeke, 1866). H = humerus; R = radius; C = cubitus

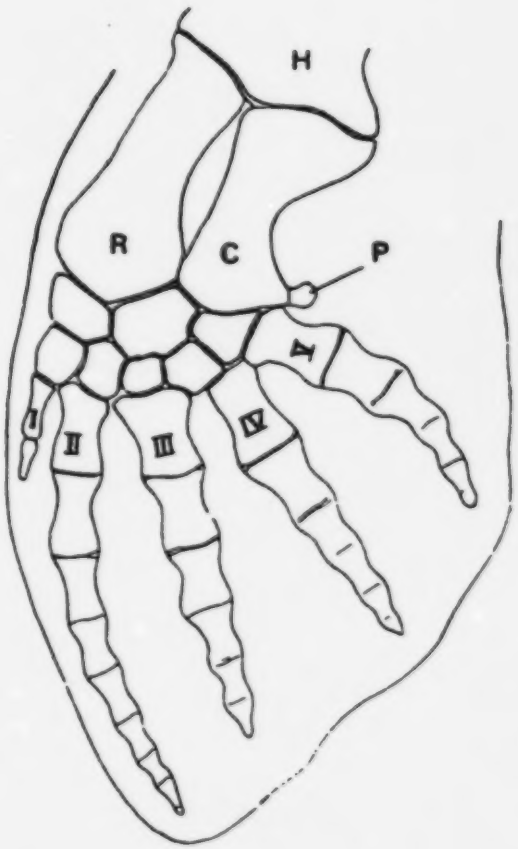

Fig. 29 — Ebauche des os de la nageoire pectorale, chez un fœtus de narval, d'après Leboucq (1889). H : humérus; R : radius; C : cubitus; P : pisiforme; I, II, III, IV et V : métacarpiens.

Fig. 29. Primordia of pectoral flipper bones in a narwhal foetus (After Leboucq, 1889). H = humerus; R = radius; C = cubitus; P = pisiform bone; I, II, III, IV, and V = metacarpals

(2) Muscle System

1) Cephalothoracic Muscles

The cephalothoracic muscle system comprises the following: hyoid, monogastric, mylohyoid, hypoglossus, genioglossus, sternomastoid, sternothyroid, mastocapsular, mastohumeral, sternohyoid, thyrohyoid, cricothyroid, ceratohyoid, geniohyoid and scalene muscles. All of these muscles occur in pairs and are symmetrical. Each scalene muscle is tripartite. Some cephalic and thoracic muscles insert on the sternum (Fig. 31):

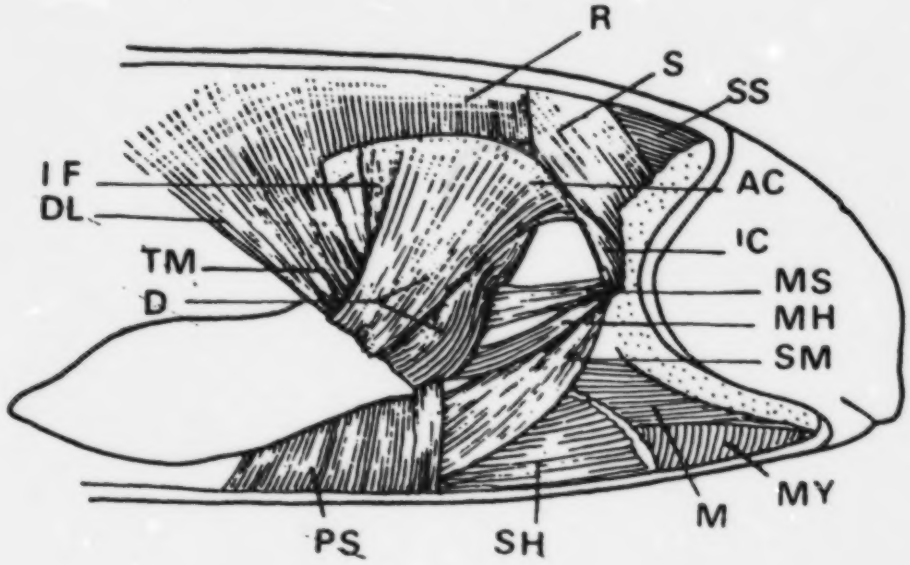

Fig. 30 — Muscles superficiels thoraciques, vus de droite, chez un fœtus de narval de 1,563 m de long, d'après Howell (1930). IF : infra-spinal; DL : dorso-latéral; TM : *teres* majeur; D : deltoïde; PS : pectoral superficiel; SH : sterno-hyoïdien; M : *monogastricus*, MY : mylo-hyoïdiens; SM : sterno-mastoïdien; MH : masto-scapulaire; IC : *iliocostalis capitis*; AC : *atlanto-scapularis*; SS : semi-spinal capitis; S : splénius; R : rhomboïde.

Fig. 30. Superficial thoracic muscles in a narwhal, foetus, 1,563 m long. Right view. (After Howell, 1930). IF = infraspinous muscle; DL = dorsolateral muscle; TM = teres major muscle; D = deltoid muscle; PS = superficial pectoral muscle; SH = sternohyoid muscle; M = musculus monogastricus; MY = mylohyoid muscles; SM = sternomastoid muscle; MH = masto-scapular muscle; IC = musculus iliocostalis capitis; AC = musculus atlantoscapularis; SS = musculus semispinalis capitis. S = splenius muscle; R = rhomboid muscle.

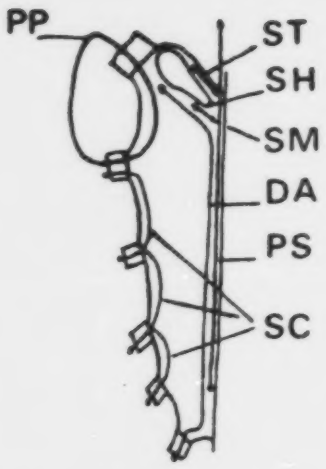

Fig. 31 — Schéma de l'insertion des muscles sur le sternum du narval, chez un fœtus de 1,563 m de long d'après Howell (1930). PP : pectoral profond; ST : sterno-thyroïdiens; SH : sterno-hyoïdien; SM : sterno-mastoïdien; DA : droit abdominal; PS : pectoral superficiel; SC : sterno-costaux.

Fig. 31. Diagram of muscle insertions on the sternum in a foetus, 1,563 m long (After Howell, 1930). PP = deep pectoral muscle; ST = sternothyroid muscles; SH = sternohyoid muscle; SM = sternomastoid muscle; DA = right abdominal muscle; PS = superficial pectoral muscle; SC = sterno-costal muscles.

2) Thoracic Muscles

The muscles of the thorax include a panniculus carnosus which extends from the surface to the deep layers and which is continuous with the sphincter colli (Fig. 13, 26, 30). Beneath the panniculus carnosus, the superficial pectoral muscle is divided into strips by oil saccules which are peculiar to the narwhal. The pectoral muscle originates at the medioventral line, covers the sternum and terminates medially on the pectoral flipper close to where the humerus articulates with the cubitus-radius.

The deep pectoral muscle is virtually cylindrical. It is attached to the first and second costal cartilages and the nearby portion of the sternum and inserts on the medial border of the coracoid process. The musculus serratus magnus, which originates at the second to the sixth ribs, develops into a fascia which disappears from view before emerging at the coracovertebral angle of the sca-

pula. It inserts on the vertebral margin. The external intercostal muscles extend from the ribs to the costal cartilage. The sternocostal muscles have a uniform surface and occupy the spaces between the fifth and second costal cartilages and the adjacent margin of sternum. Some fibers extend through only a single intercostal space, whereas others occupy two spaces.

3) Abdominal Muscles

The abdominal muscles include two large straight muscles, situated on either side of the median line, two external oblique muscles, two internal oblique muscles and one transverse abdominal muscle. The first of these muscles originate at the posterior sternum and disappear from view in fibrofatty tissue anterior to the vulva. The dorsal vertebral muscles include the musculus latissimus dorsi (or great dorsal muscle), the rhomboid muscle, the atlantoscapular muscle, which elevates the angle of the scapula, the slender splenius muscle, aponeurotic sheets, which bury the lumbocaudal portion of the long vertebral muscles, the musculi erectores spinae, the musculi longissimi capitis and musculi recti capitis superiores. Little is known about the perineal muscles. Revision of their classification is in order as it is rationally impossible to distinguish a pelvis in a cetacean. In the narwhal, in particular, one cannot rightly speak of the pubic, iliac or ischiatic segments of the abdominal bone (Arvy, 1976), with the result that the nomenclature for all the posterior abdominal muscles needs to be standardized. This means abandoning the terms "iliobliquus," "puboventralis,"

"ischiocaudalis," and "ilioabdominis" when referring to the muscles. It may be decided to retain the terms "levator vulvae," levator ani," and "retractor ani" for the muscles identified by Howell (1930) in a female foetus, 1.563 m long. This is the only specimen to have been examined in this manner. A comparative study using a male foetus would naturally be of fundamental interest. The best guide would be the distribution of terminal spinal nerves.

4) Pectoral Flipper Muscles

The deltoid muscle is one of the strongest muscles occurring in the pectoral flipper. It is a complex muscle which originates on a large aponeurosis attached to the cranial three-quarters of the cartilaginous vertebral border of the scapula and the ventral bony border of the acromion. It consists of two parts: the upper, thin part lies over a thicker part. The two layers may be easily separated along the cranial border. The superficial muscle fibers produce tendon-like bands which converge toward the cubital border of the humerus. The deep portion of the deltoid muscle is massive, especially on the cranial side, and the deepest fibers are intimately connected with the periosteum of the craniodorsal third of the scapula. They completely cover the acromial and coracoid processes (Fig. 32).

The supraspinous mucle originates at the coracoventral angle of the scapula and the medial side of the acromial process under which it passes. It is relatively thick but narrow. It inserts on the cranial portion of the humeral head, just behind the insertion of the mastohumeralis muscle.

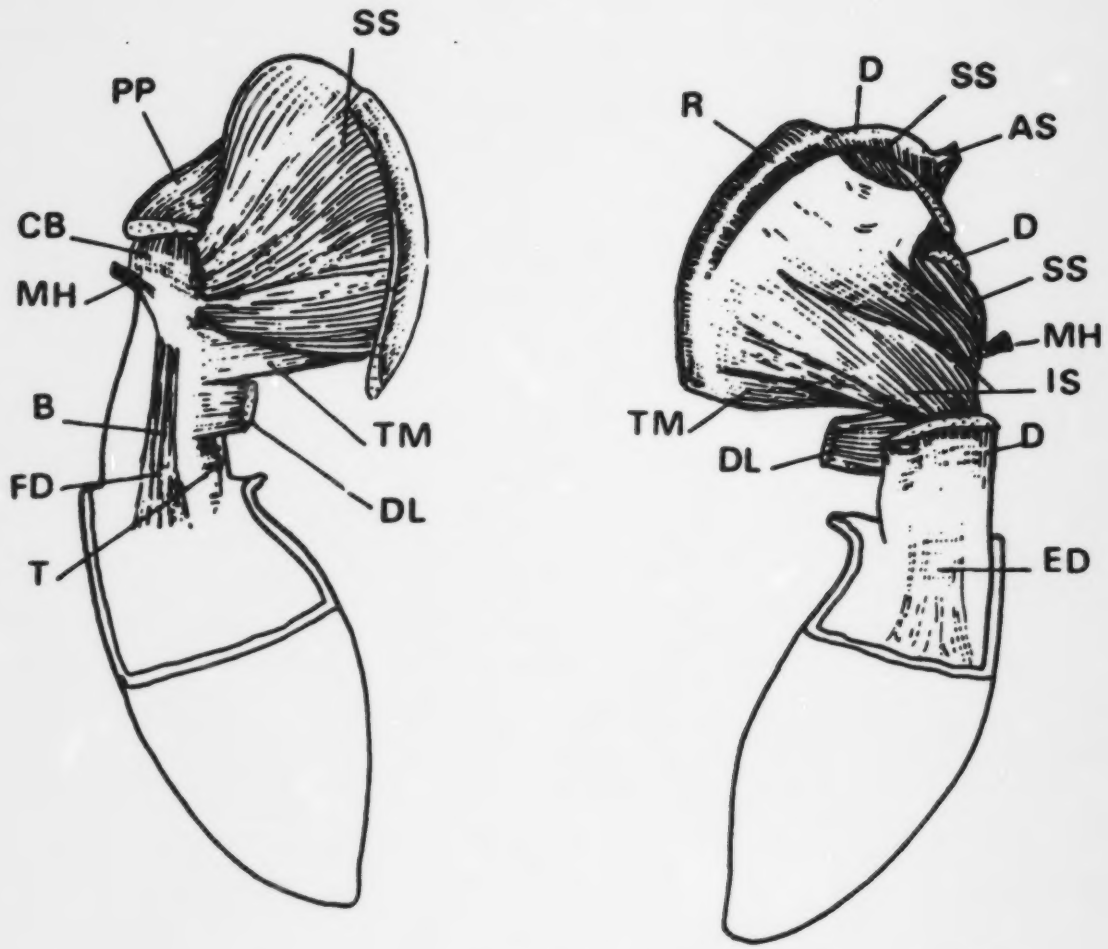

Fig. 32. Muscles of the pectoral flipper in a foetus, 1.563 m long (After Howell, 1930). medial view, left, and lateral view, right. Left: PP = deep pectoral muscle; CB = coracobrachial muscle; MH = mastohumeral muscle; B = biceps muscle; FD = flexor muscle of fingers; T = triceps muscle; DL = dorsolateral mucle; TM = teres major muscle; SS = subscapular muscle. Right: D = deltoid muscle; R = rhomboid muscle; TM = teres major muscle; DL = dorsolateral muscle; ED = extensor muscle of fingers; D = deltoid muscle; MH = mastohumeral muscle; IS = infraspinous muscle; SS = supraspinous muscle; AS = atlantoscapular muscle.

The infraspinous muscle covers roughly half of the scapula. It originates on the periosteum of the caudal third of the vertebral border of the scapula and extends to the base of the coracoid process. The cranial portion consists of two tenuous superficial strips.

The teres major muscle originates at the glenovertebral angle of the scapula and inserts along the medial crest of the humerus.

The subscapular muscle is fleshy on the surface but the internal portion is aponeurotic, fanning out. It inserts in the proximal area of the lesser tuberosity of the humerus.

The coracobrachial muscle is small. The widest portion lies under the insertion of the deep pectoral muscle. Its origin is on the ventral border of the coracoid process and its site of insertion on the lesser tuberosity of the humerus.

The pectoral flipper muscles proper may be assigned to one of three groups: the triceps, the tripartite scalene and the biceps muscles. In addition, there are muscle fibers that connect to the carpal and metacarpal bones and the phalanges, but they are arranged in thin sheets and it is not possible to distinguish between the flexor and extensor muscles of the fingers.

4. THE ORGANS IN THE NARWHAL

A. The Heart and Breschet's Rete Mirabile in the Thorax

In 1836, the anatomist, Gilbert Breschet, gave an admirable description of an extremely large vascular complex in the thorax that is unique to mammals. This system was studied in detail in porpoises and was also observed in Delphinus delphis, Delphinus globiceps and in a Balaena mysticetus foetus

Forty years later, it was realized (Wilson, 1879) that the narwhal was endowed with a like vascular complex. In 1861, the master of the steamer, "Narwhal," from Dundee caught a gravid female north of the Davis Strait. The foetus was 64¼ inches in length and 48½ at its maximum circumference. The animal was fixed and

Wilson (1879) studied the arterial rete mirabile of the thorax. Since then, there have been no studies of this nature in narwhal foetuses of different ages or in adult specimens, for that matter (Fig. 33 and 34).

The network is of a type found in cetaceans and there is no equivalent in any other aquatic mammal. In addition, it is related (Fig. 34), but not identical, to systems that have been described since Breschet (1836).

It is not farfetched to assume that the narwhal, like other cetaceans, has other retia mirabilia besides the one in the thorax, i.e., arterial: mammaries, dorsal peritoneal; venous: in the psoas, genital tract, . but apparently there has been no research in this area.

Furthermore, there have been no studies to date on the rete mirabile in the adult narwhal.

The heart of an adult caught in Spitzberg in 1817 weighed 11 pounds. Ninety minutes after the animal's death, the temperature of the blood was 97^{o}C. This seems to be the extent of our information on the heart and blood.

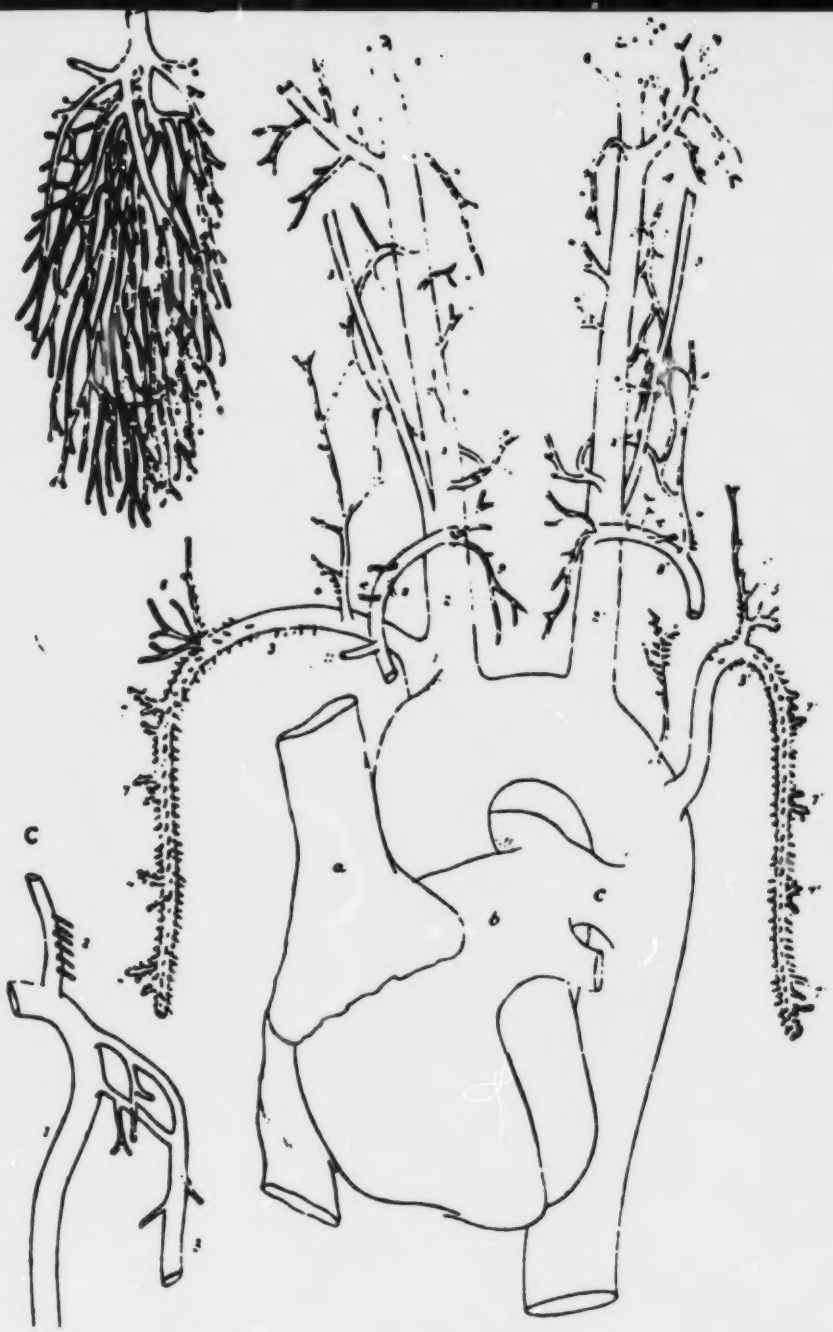

Fig. 33. Vascularization in the narwhal. Top left: diagram of the cluster of arterial branches arising from the internal mammary artery. They pass around and among the pectoral muscle bundles. Center: heart, aortic arch with branches. 1. innominate artery 2. trunk of right carotid artery 3. posterior thoracic branch 4. ascending cervical branch 6. first intercostal arteries. 7. other intercostal arteries 8. cervical arterial segment arising from the internal mammary artery 9. posterior thyroid branch 10. arterial branches supplying the right cervical muscles 11. axillary arterial branch 12. external carotid branch 13. internal carotid branch 14. arterial branches supplying the anterior, lateral and posterior neck muscles. 15. pharyngeal arterial branch 16. laryngeal arterial branch 17. occipital branch 18. lingual branch. Bottom left: the large arteries giving rise to branches that join to form a single trunk. 1. left internal mammary artery 2. left cervical ascending artery 3. left axillary artery. (After Wilson, 1879).

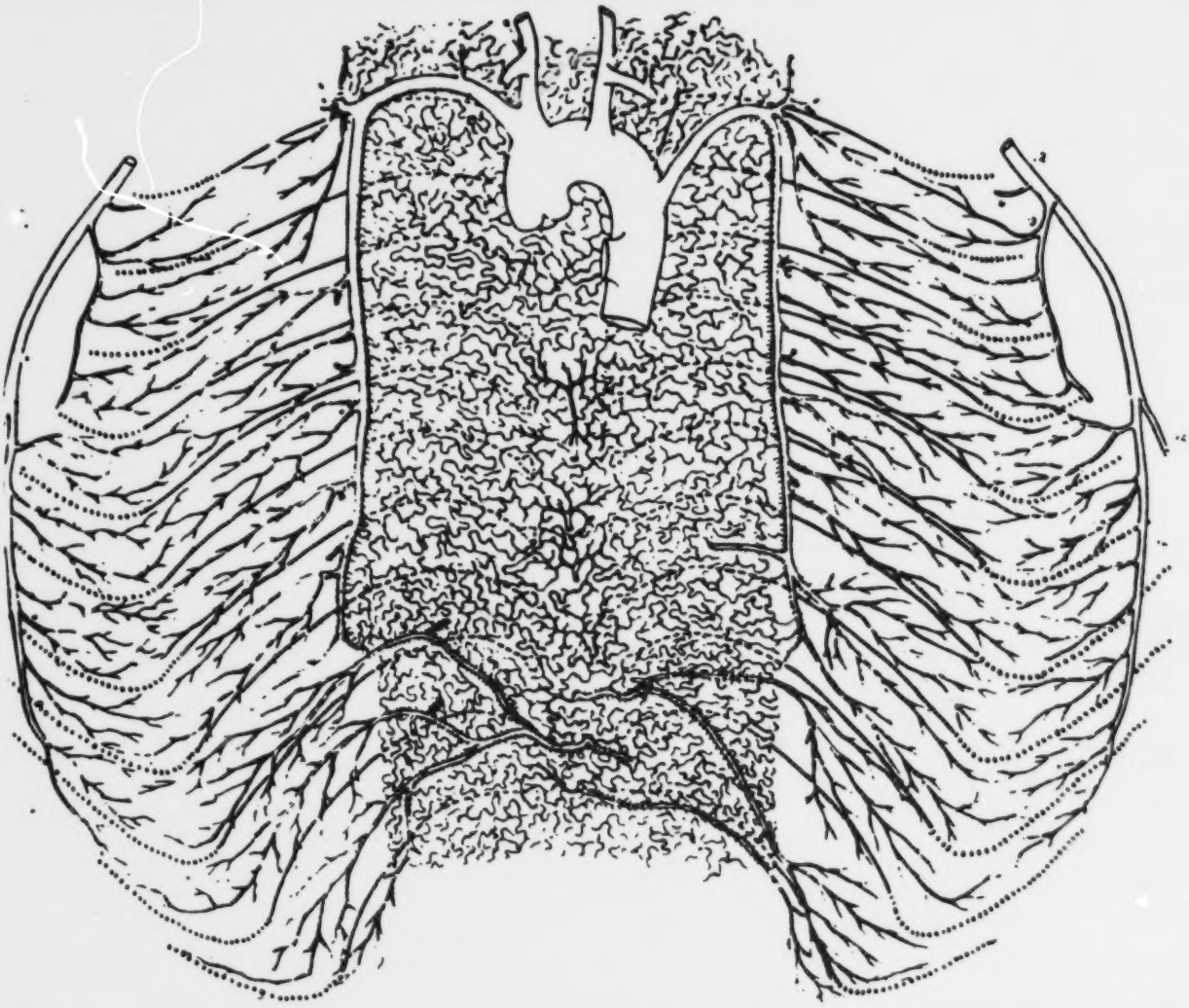

Fig. 34. Diagram of the arterial rete mirabile in the thorax with the origins and relationships with the ribs and intercostal spaces following removal of the heart and thoracic aorta. The ribs are indicated by solid and dotted lines. 12. intrathoracic segment of the internal mammary artery 13. its sternal branch 14. its thymic segment 15. its anterior epigastric branch 16. its musculophrenic branch (After H.S. Wilson).

Fig. 34 : Schéma du plexus artériel admirable thoracique, de ses origines et de ses rapports avec les côtes et les espaces intercostaux, après résection du cœur et de l'aorte thoracique, chez le narval. Les côtes sont partiellement en trait plein et partiellement en pointillé. 12 : segment intra-thoracique de l'artère mammaire interne; 13 : son rameau sternal; 14 : son segment thymique; 15 : son rameau épigastrique antérieur; 16 : son rameau musculo-phrénique (D'après H.S. Wilson).

1) The Arcus Aortae and Its Branches

In the narwhal, the arcus aortae, seen from the front, is masked by the pulmonary artery. Only a narrow strip appears above the artery. The remainder is buried under the lobes of the thymus. The right thymic lobe separates the aorta from the anterior vena cava. The two thymic lobes separate the arcus aortae from the pneumogastric nerves. Removal of the thymus permits a better view of the rostral portion of the aorta, on the right, which slants upward in a curve, then to the left of the spinal column. After the aorta emerges from the left ventricle, it gives rise to the coronary arteries. The innominate arteries, the left carotid trunk and the left posterior thoracic artery arise from the convex portion of the aorta (Fig. 33).

The innominate artery, the largest of the arteries, arises from the initial portion of the transverse segment of the arch, at the level of the first ribs. It extends for about one-half inch towards the neck and then divides into two large branches: the right posterior thoracic artery follows a horizontal course towards the first rib and the right carotid trunk, which it meets approximately 3 inches from the spinal column. It then curves sharply to the back and continues along the internal border of the thoracic wall. It passes the first eight ribs and terminates at the level of the eighth intercostal space. It therefore consists of two segments: a short and arch-shaped cervical segment and a terminal costal, intrathoracic segment.

The cervical arciform segment comes in contact with the innominate vein, the pneumogastric nerve, sympathetic reticula, the phrenic nerves and the scalene muscle. On the surface, it is covered by the cervical portion of the right thymic lobe. At the point where the artery crosses the right innominate, vein, it gives rise to a short cervical branch which anastomoses with the anterior thyroid artery and pharyngeal arteries emerging from the external carotid. On the left, this arterial branch arises from the left internal mammary artery.

The costal intrathoracic segment is partially embedded in the thoracic network and runs along it, parallel to the spinal column. Shortly before it ends, it divides into numerous branches. Hundreds of these are oriented in the direction of the column. They are long and slender and similar, if not identical, in caliber. They are continuous with the network. Other branches are oriented toward the exterior and, except for the first one, are grouped to occupy the intercostal spaces (3rd to the 8th). The first group may be seen before the artery enters the thorax. It is larger than the other groups and is made up of numerous branches, some of which are directed toward the front (to supply the cervical muscles) and others, toward the back (to supply the 1st and 2nd intercostal spaces). The other groups supply the other intercostal spaces.

The right carotid trunk supplies only a few branches to the thoracic arterial system. It gives rise to the cervical arteries.

The left carotid trunk arises from the arcus aortae near (3/4 inch) the innominate artery. It is only slightly smaller in caliber. It is oriented toward the front and slightly toward the exterior. In the thorax, it is external to the left thymic lobe which separates it from the left pneumogastric nerve. It comes in contact with the thyroid gland.

The posterior left thoracic artery arises immediately in front of the ductus arteriosus, 1.5 inches from the left carotid trunk. It proceeds toward the front, near the first rib, then curves toward the back to terminate in the 9th intercostal space. The arch is short and situated within the thorax. Toward the front, it gives rise to only one branch which divides into a group of arterioles near the 1st rib. Toward the back, it gives rise to an entire series of arteries, some of which within, others outside, the network. These arteries supply the intercostal spaces.

The thymic artery. Between the sites of origin of the left carotid trunk and the left posterior thoracic artery (but closer to the latter), the arcus aorta gives origin to an artery which is oriented toward the front. This artery in turn gives rise to a branch supplying the left thymic lobe before disappearing from view in the left portion of the rete mirabile.

2) The Descending Aorta

Above the diaphragm, the descending aorta gives rise to seven intercostal branches from its spinal border. These branches vary in size, with the first four becoming progressively smaller. The last three branches are larger. The first branches describe an an arc toward the front, and the last two are directed toward the back. Each branch divides into two lateral branches. All of these arteries have numerous and varied ramifications, but as the latter have been observed in only one foetal specimen, it cannot be assumed they occur in just this way in foetuses of different stages of development or even in adult males or females. Rather than dwell on further details, we prefer to refer the reader to the figures (Fig. 34).

These are the original arterial trunks of the thoracic network in the narwhal. All of the arterial ramifications between the right and left systems follow a tortuous course, anastomosing to form an extensive vascular network that is uniform in appearance because the vessels are the same in caliber. The whole system is unique among mammals, and it is strange that it has not aroused any interest over the past one hundred years (Wilson, 1879).

B. The Tongue, Larynx, Trachea and Lungs

1) The Tongue

The tongue is long, round and closely connected to the mandible at its distal end. The base contains numerous openings of all shapes that exude a mucus-rich secretion (Fleming, 1806).

In a female specimen caught in the Zuider Zee, near Harderwijk, in 1921, the tongue was relatively small, i.e., only 33 x 8 cm from the tip of the tongue to the base of the epiglottis, with the tongue proper accounting for only 14 cm. The posterior area was actually more pharyngeal than lingual in nature. The upper side was perfectly smooth and yellowish white. The margins were regular and devoid of any fringed appendages. There were no traces of lingual pupillae. This particular specimen had no frenum, but the tip was not free. A transverse groove marked the separation between the lingual and pharyngeal mucosae. The mucosa in front of the groove was yellowish, whereas that behind the groove was red, porous and rough with folds and crevices, indicating the site of junction of pharyngeal salivary glands.

In a female foetus, 1.563 m long, examined by Howell (1930), the styloglossus muscle extended from the middle of the stylohyal process, whereas the entire basihyal bone gave origin to the hyoglossus muscle. The fibers of the latter converged to become medial in relation to the styloglossus muscle, then passed under the genioglossus muscle and terminated at the tongue. The ceratohyal horn and genioglossus muscle were difficult to distinguish. They were not attached to the hyoid bone.

2) The Larynx

We owe whatever data we have on the narwhal larynx to a few studies on the skeleton and its associated muscles (Mayer, 1851; Hein, 1914; Howell, 1930) (Fig. 35-39).

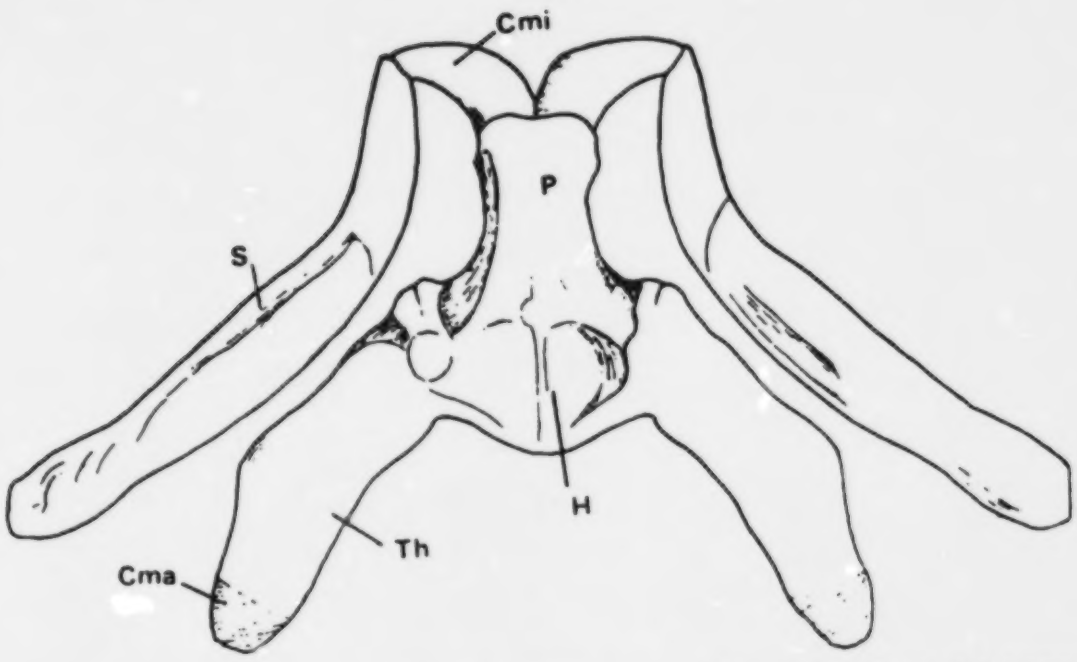

Fig. 35. Hyoid system in the narwhal. H = body of hyoid bone; P = processus lingualis; Cmi and Cma = cornu minus and cornu majus; S = stylohyal process.

Following dissection, the hyoid bone appears to consist of five parts. A central trunk or hyoid body branches out on four sides (Fig. 35-36).

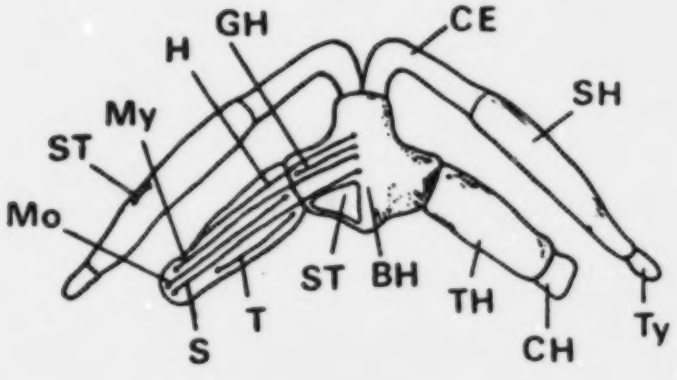

Fig. 36 — Schéma du complexe hyoïdien avec les insertions musculaires, chez un fœtus de narval de 1,563 m de long. (D'après Howell, 1930). CE : cérato-épihyal; SH : stylohyal; Ty : cartilage tympanohyal; CH : chondrohyal; TH : thyrohyal; BH : basihyal; ST : sternothyroïdien; T : thyréohyoïdien; S : sternohyoïdien; Mo : monogastrique; ST : stylohyoïdien; My : mylohyoïdien; H : hyoglosse; GH : géniohyoïdien.

Fig. 36. Diagram of the hyoid complex with muscle insertions in a narwhal foetus, 1.563 m long (After Howell, 1930). CE = cerato-epihyal horn; SH = stylohyal process; Ty = tympanohyal cartilage; CH = chondrohyal cartilage; TH = thyrohyal process; BH = basihyal bone; ST = sternothyroid muscle; T = thyrohyoid muscle; S = sternohyoid muscle; Mo = monogastric muscle; ST = stylohyoid muscle; My = mylohyoid muscle; H = hyoglossus muscle; GH = geniohyoid muscle.

The thyroid cartilage is made up of three parts. The middle portion is hexagonal and concave on the ventral side. It constitutes the body of the thyroid cartilage and is extended on either side by cartilage. The central area consists of bone (Fig. 37).

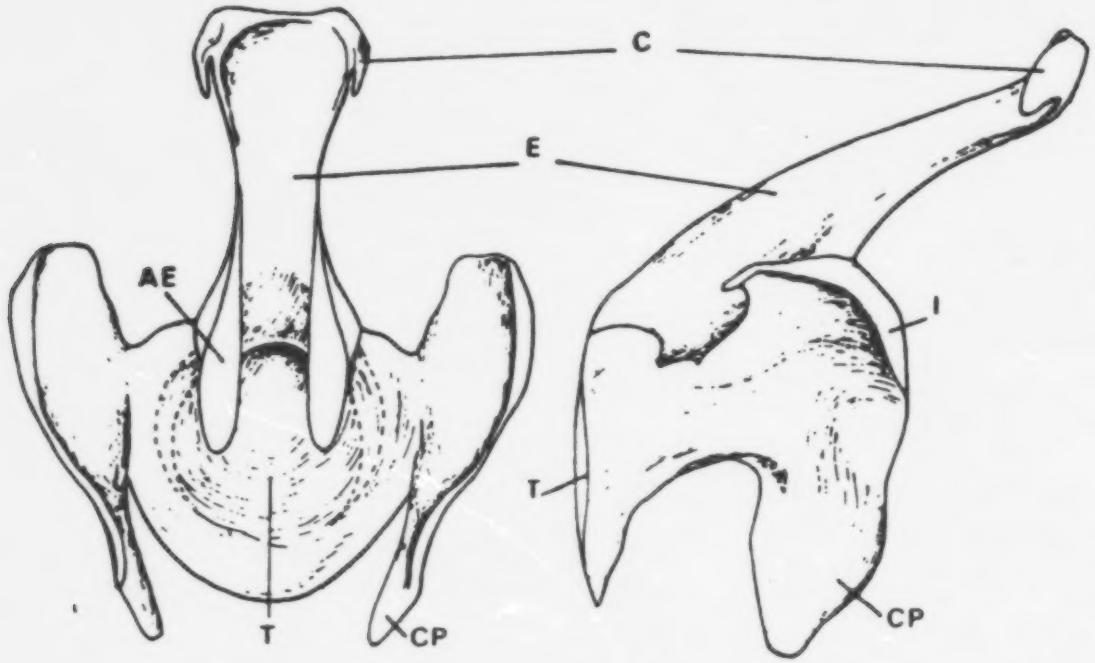

Fig. 37. Left, dorsal view, and right, lateral view of the thyroid and epiglottic cartilages in the narwhal. C = cartilaginous ring at the dorsal extremity of the epiglottis; E = epiglottis; T = thyroid cartilage; AE = lateral wing of the epiglottis; CP = posterior horn of the thyroid cartilage; I = insertion of the superior constrictor muscle of the pharynx (After Hein, 1914).

The arytenoid cartilage includes a) a basal median portion, which is articulated with the cricoid cartilage via a longitudinal furrow, b) a dorsal extension or anterior horn, and c) a ventral projection or posterior horn. It is connected to the tips of the lateral wings of the epiglottis (Fig. 38-39). The hyoid complex comprises numerous lamellar muscles which are more or less aligned above one another (Fig. 36).

See page 58 a.

Fig. 38. The arytenoid cartilage in the narwhal. CA = anterior horn; A = arytenoid cartilage; FA = articular side (After Hein, 1914).

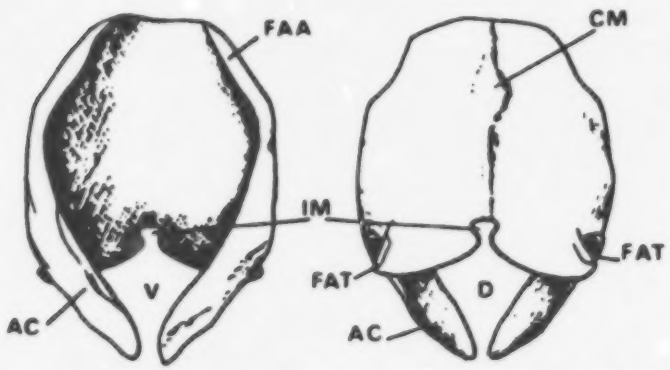

Fig. 39. The cricoid cartilage, ventral view (V) and dorsal view (D). FAA = articular side of the arytenoid cartilage; IM = median incisure of the cricoid cartilage; AC = arc of cricoid cartilage; FAT = articular side for the thyroid cartilage; CM = median muscle crest of the cricoid cartilage (After Hein, 1914).

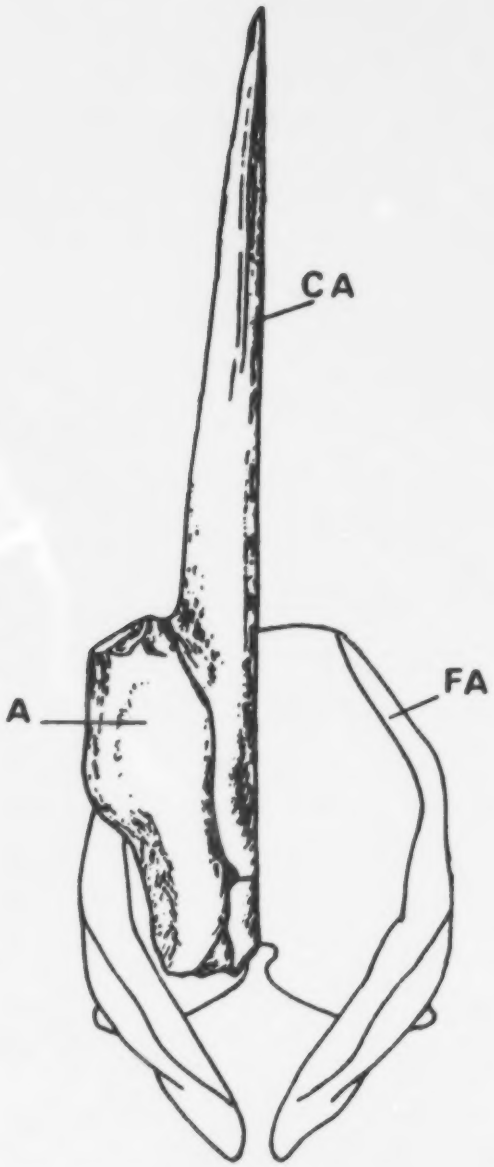

Fig. 38 — Schéma de l'aryténoïde du narval. CA : corne antérieure; A : aryténoïde; FA : face articulaire. (D'après Hein, 1914).

Fig. 38. The arytenoid cartilage in the narwhal. CA = anterior horn; A = arytenoid cartilage; FA = articular side (After Hein, 1914).

3) The Trachea and Lungs

All of the tracheal rings are closed except for the first one which is open on the ventral side. The trachea divides into four bronchi which lead into the lungs. The latter are non-lobate (Fleming, 1808).

The entire linguopharyngolaryngeal area has a highly developed muscle system. Hein (1914) distinguished the following muscle bundles on dissection: hylohyoid, digastric, sternohyoid, styloglossus, hyoglossus, genioglossus, palatoglossus, hyopalatine, hyostyloid, thyrohyoid, cricothyroid, hyo-epiglottic, posterior cricoarytenoid, thyroarytenoid, lateral cricoarytenoid, and transverse arytenoid.

C. The Digestive Tube

The narwhal digestive tube was studied by Woodhead and Gray (1888), Turner (1889), Jungklaus (1898) and Hein (1914).

The Stomach

When seen from the exterior, the stomach gives the impression of being trilocular when, in actual fact, it has five compartments. The third compartment is by far the smallest (Fig. 40).

Fig. 40 -- Schéma du système digestif du Narval: en haut : vue d'ensemble: en bas à gauche coupe longitudinale: à droite, coupe transversale. 1er estomac: 2 à 5 : 2ème, 3ème, 4ème et 5ème estomac: 6 : ampoule duodénale: 7 : duodénum: P : tête du pancréas: R : rate: L : ligament hépato-duodénal: E : grand épiploon: D : diaphragme: S : séreuse péritonéale. (D'après Hein).

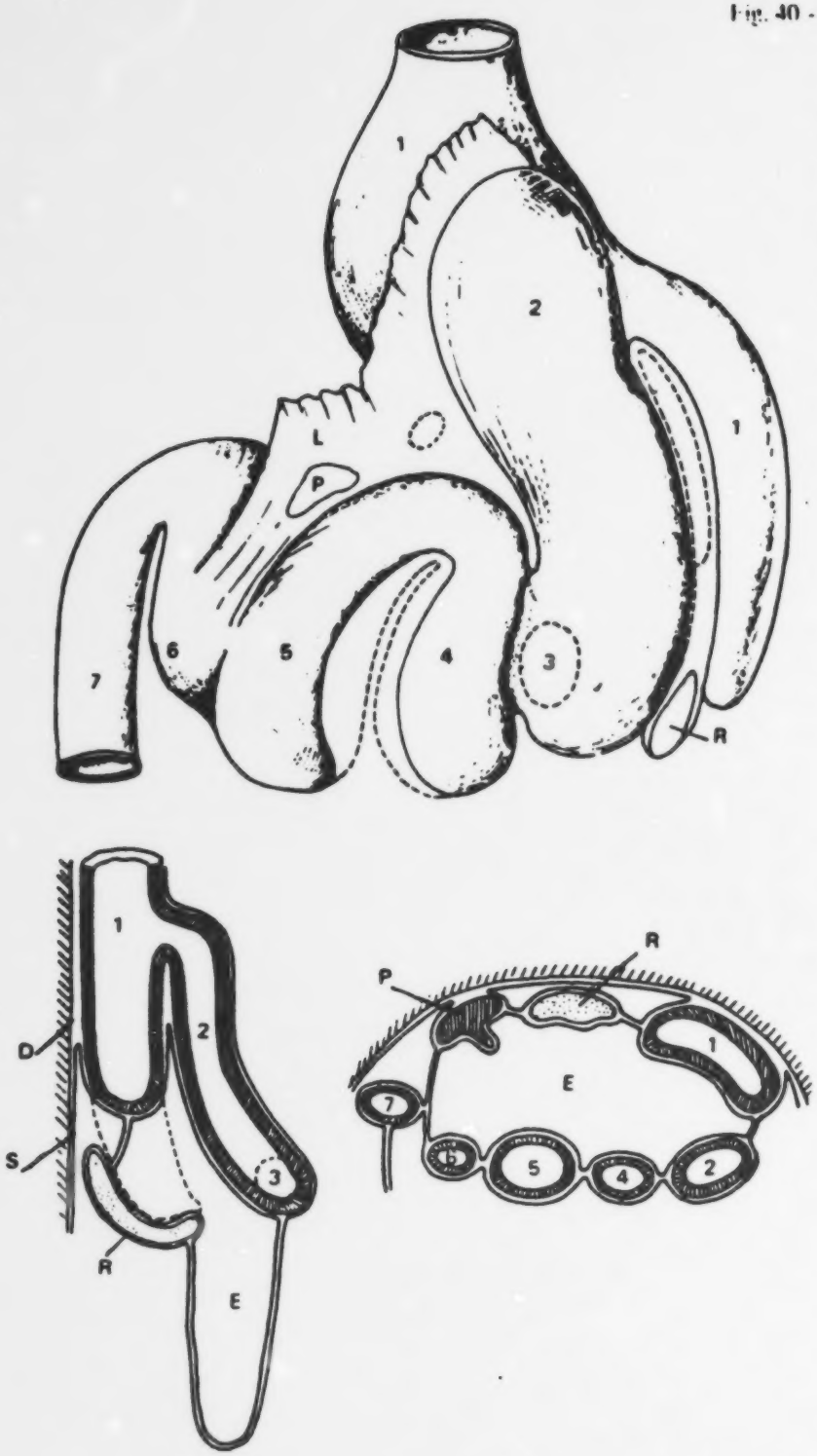

Fig. 40. The narwhal digestive tract. Top: overall view. Bottom left: longitudinal section. Bottom right: cross section. 1 = first stomach; 2-5 = second, third, fourth and fifth stomachs; 6 = duodenal ampulla; 7 = duodenum; P = pancreas head; R = spleen; L = hepatoduodenal ligament; E = greater omentum; D = diaphragm; S = peritoneal serosa (After Hein).

The first stomach is S-shaped with a spacious, bulb-like rostral area anterior to the diaphragm. A distal diverticulum tapers toward the rear, forming a cecum which is covered by the peritoneum.

The second stomach lies against the ventral side of the first stomach. Its major axis is parallel to the axis of the body, except in the case of the terminal portion which curves to the right and continues into the third gastric pouch.

As the third stomach is situated dorsally in relation to the caudal extremity of the second stomach, it is hidden on frontal view, and the second stomach seems to lead into the fourth. It was found that in a specimen in which the first stomach was 40 cm long, the third stomach was only 8 cm long. This third stomach is oval (8 x 4 cm).

The fourth and fifth stomachs are the same size. They are half as long as the second stomach but just as wide. The fourth and fifth stomachs lie parallel to each other in a horsehoe arrangement. They are separated by a constriction of approximately 8 mm.

The duodenum is separated from the stomach by a shallow furrow. It lies first along a rostral axis, but then, curves abruptly toward the back. It has a thin wall which distinguishes it from the rest of the intestine into which it gradually extends. The pylorus is approximately 14 mm in diameter.

The gastroduodenal mucosa is thickest in the first stomach where it covers longitudinal muscle bundles. Only in the fifth stomach is the wall flexible and elastic and so thin that the parietal vessels may be seen through the serous membrane.

The first stomach wall is yellowish in colour and remarkably thick (7 mm). The mucosa has a number of either grouped or scattered elevations that are cone-shaped, pointed and hard, forming true stomach denticles. They have been reported by Junklaus (loc. cit., p 33), and Woodhead and Gray (1888, p. 795). The second stomach wall is as thick as the first, but the mucosa, in contrast, is brownish red with longitudinal folds and scattered minute furrows and elevations. The third stomach wall is slightly thicker than the first two. The mucosa is brownish red and has folds. The fourth stomach wall is not very thick (4 mm). The mucosa is greenish and smooth without any folds. The wall of the fifth stomach is similar although half as thick (2 to 2.5 mm).

The mucosa of the first duodenal segment is smooth without any folds, but after the duodenal curve, it has pronounced circular folds that project roughly 2 mm into the duodenal lumen.

The Peritoneum

The peritoneum invests the spleen, most of the pancreas and all of the gastric pouches, with the exception of the portion of the stomach lying anterior to the diaphragm. It contains little fat tissue and is abundantly supplied with vessels. The arterial,

venous and lymphatic vessels have not yet been identified, and it is not known whether Aselli's pancreas or Peyer's patches occur in the narwhal.

The Spleen and Pancreas

The spleen is located at the same level as the first gastric pouch. It has a flattened heart shape. The dorsal side is convex; the ventral side, concave. The length corresponds to its maximum width, i.e., 10.5 cm. The concave side is divided into two unequal parts by a longitudinal ridge. The right and wider portion is retroperitoneal, whereas the left portion is not invested by the serous membrane (Hein, 1914).

The pancreas is dorsal to the fifth gastric pouch.

The hepatopancreatic canal occurs above the fifth stomach and crosses the duodenal wall obliquely (Hein, 1914). Like all other cetaceans, the narwhal does not have a gall bladder.

D. The Endocrine Glands

The endocrine glands have not been systematically studied and little is known about them (Arvy , 1971).

The Hypophysis

Eales (1950) located the hypophysis on serial cross sections of a foetal head. (Fig. 41).

See page 64 a.

Fig. 41. Diagram of a cross section of a foetal head at the level of the pituitary gland (After Eales, 1950).

ip.l = median anterior interparietal bone
occ = orbitocapsular commissure
h = adenohypophysis
h = alisphenoid
at = temporal wing
p = basal or parachordal plate
vb = vomer
Et = Eustachian tube
nph = nasopharynx
bl = subcutaneous fat tissue
Mc = Meckel's cartilage
b = buccal cavity
ce = cerebral hemisphere
par = parietal bone
G = Gasser's ganglion
ptg = pterygoid bone
lj = lacrymojugal bone
VII = facial nerve
Vcd = inferior dental branch of the trigeminal nerve
Vcmh = mylohyoid branch of the trigeminal nerve
den = dental bone

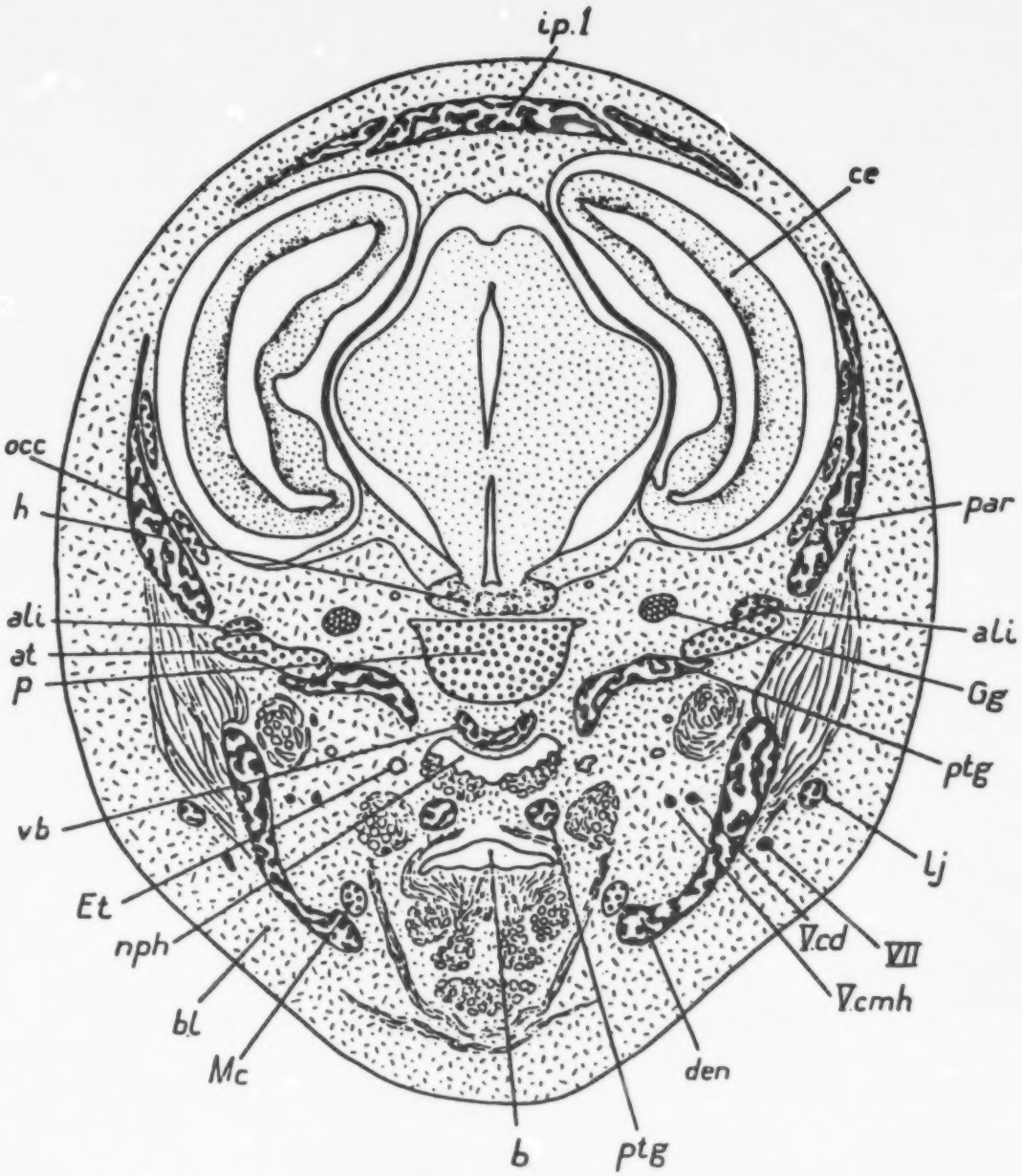

Fig. 41 — Schéma d'une coupe transversale de la tête d'un foetus de narval, passant à la hauteur de la glande pituitaire. (D'après Eales, 1950).

ip.l	= os interpariétal antérieur médian	h	= cavité buccale
occ	= commissure orbito-capsulaire	ce	hémisphère cérébral
h	= adénohypophyse	par	= os pariétal
h	= alisphénoïde	G	= ganglion de Gasser
at	= aile temporale	ptg	ptérygoïde
p	plaque basale ou parachordale	lj	= os lacrymo- jugal
vb	vomer	VII	= nerf facial
Et	trompe d'Eustache	Vcd	branche dentaire inférieure du trijumeau
nph	naso-pharynx	Vcmh	branche mylo-hyoïdienne du trijumeau
bl	tissu adipeux sous-cutané	den	= os dentaire
Mc	cartilage de Meckel		

The Thyroid

Hein (1914) found that the thyroid gland in a female specimen he examined formed an arc and was triangular in cross section. The arc was incomplete in the back and lay against the ventral side of the trachea, immediately in front of the cricothyroid and sterno-thyroid muscles. (Fig. 42).

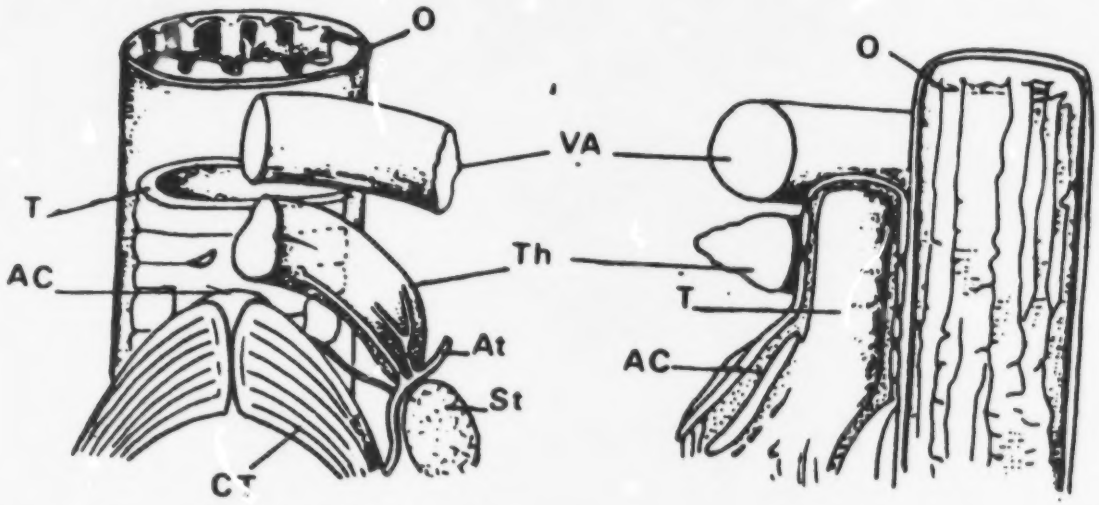

Fig. 42 — Rapports de la glande thyroïde du Narval. O : oesophage; T : trachée; VA : veine anonyme; Th : glande thyroïde, vue de face, à gauche, et sur section médiane, à droite; St : muscle sterno-thyroïdien; CT : muscle crico-thyroïdien; AC : arc cricoïdien; At : artère thyroïdienne. (D'après Hein 1914)

Fig. 42. The thyroid gland and its relation to other structures. O = esophagus; T = trachea; VA = anonymous vein; Th = thyroid gland (left, frontal view; right, median section); St = sternothyroid muscle; CT = cricothyroid muscle; AC = cricoid arch; At = thyroid artery (After Hein, 1914).

The Testicles and Adrenal glands were dissected by Meek (1918) (Fig. 43).

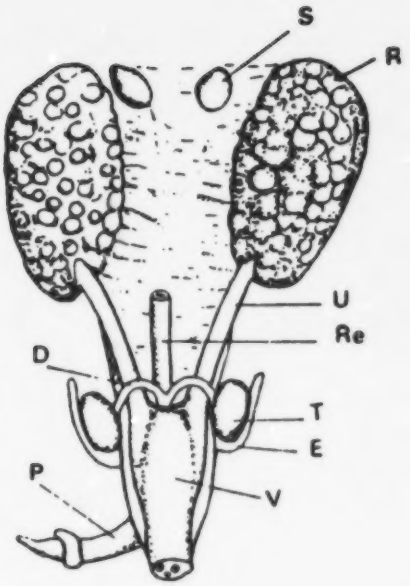

Fig. 43 — Schéma de l'appareil génito-urinaire d'un fœtus de narval. (D'après Meek, 1918). De haut en bas et de gauche à droite: S : glande surrénale; R : rein; U : uretère; Re : rectum sectionné; T : testicule; E : épididyme; V : vessie; P : pénis, court, rond et pointu; D : déférent.

Fig. 43. Urogenital tract in a foetus (After Meek, 1918). From top to bottom and left to right: S = adrenal gland; R = kidney; U = ureter; Re = sectioned rectum; T = testicle; E = epididymis; V = bladder; P = short, round and pointed penis; D = vas deferens.

The Ovaries

In the female specimen examined by Hein (1914), the left ovary was much larger than the ovary on the right (76 x 36 mm vs 65 x 28 mm). The surface of the ovary was smooth on the right but irregular on the left. In cross section, the organ was bean-shaped.

It is likely individual variations exist, as Daudt observed that the ovarian surface in an embryo he examined was rough and not smooth.

In the region of the ovary, the fallopian tube widened. The free border was smooth, semi-lunar and 9.5 cm in diameter. The infundibulum was wide. There were folds in the mucosa.

Section of the left ovary revealed an oval corpus luteum , the presence of which could not have been surmised from the exterior. It was yellowish red in colour and 10 x 8 mm.

Comments: there is a total lack of data on the parathyroid glands, the pineal body and the islands of Langerhans.

E. The Urogenital Tract

The Kidneys and Bladder

In a female specimen examined by Hein (1914), the kidneys were 30 x 15 x 6 cm. There were 198 reniculi on the ventral side and 126 on the dorsal side, i.e., a total of 324 visible reniculi on the kidney. Several showed further branching. The ureter emerged from the ventral side of the kidney near the caudal end. The renal veins and arteries entered and emerged at the rostromedial angle of the dorsal side of the kidney (Fig. 43-44).

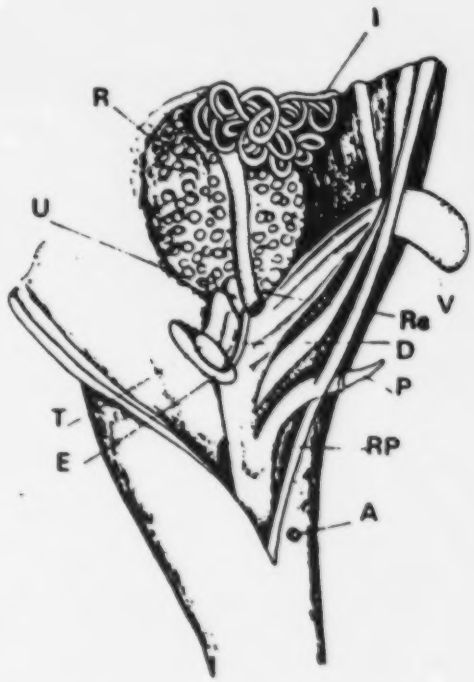

Fig 44 — Schéma d'une dissection de la région urogénitale d'un foetus ♂ de narval, d'après Meek (1918). I : intestin; V : vessie; Re : rectum; D : déférent; P : pénis; RP : rétracteur du pénis; A : anus; E : epididyme; T : testicule; U : uretère; R : rein, avec ses rénicules.

Fig. 44. Diagram of the dissected urogenital area in a male foetus (After Meek, 1918). I = intestine; V = bladder; Re = rectum; D = vas deferens; P = penis; RP = penis retractor muscle; A = anus; E = epididymus; T = testicle; U = ureter; R = kidney with reniculi.

The bladder is pear-shaped with a thick wall (Hein, 1914; Meek, 1918). It dilates little when injected with air. The ureters open into the bladder at points far down on the structure. The orifices are surrounded by arciform folds. The ureters are 8 mm across, the wall accounting for 6 mm. The mucosa is smooth with longitudinal folds. The urethra is 25 cm long. At a distance of 25 mm from the external orifice of the urethra, the urethral lumen widens into a navicular fossa (Fig. 45).

At the summit of the bladder, a 1-cm-deep recess forms a blind pouch in a median umbilical ligament which probably represents what remains of the urachus.

See page 68 a.

Fig. 45. Terminal portion of the urinary tract. RO = the remains of the urachus; U = ureter; V = bladder; CT = triangular field where longitudinal folds are continuous with the circular folds of the bladder; OU = orifice of ureter; UI = internal orifice of urethra; UE = external orifice of urethra; FN = navicular fossa

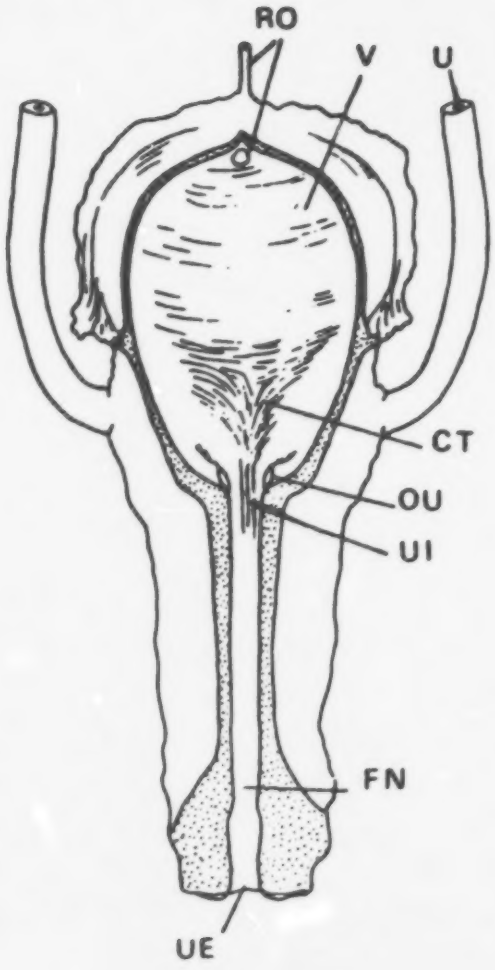

Fig. 45 — Partie terminale du système urinaire. RO : reste de l'ouraque; U : uretère; V : vessie; CT : champ trangulaire, où les plis longitudinaux se mettent en continuité avec les plis circulaires de la vessie; OU : orifice uretéral; UI : orifice urétral interne; UE : orifice urétral externe; FN : fosse naviculaire.

Fig. 45. Terminal portion of the urinary tract. RO = the remains of the urachus; U = ureter; V = bladder; CT = triangular field where longitudinal folds are continuous with the circular folds of the bladder; OU = orifice of ureter; UI = internal orifice of urethra; UE = external orifice of urethra; FN = navicular fossa

See page 69 a.

Fig. 46. Longitudinal section (right half seen from the left side) of the vestibule of the vagina, bladder and rectum. CU = horn of uterus; O = ovary; M = mesentery; R = rectum; FRU = rectouterine cleft; UR = ureter; P = transverse vesical fold; V = bladder; OU = orifice of urethra; OV = vaginal orifice; A = anus; U = uterus.

The Genital Tract

a) In the Male

Meek (1918) was apparently the only anatomist to examine the genital tract in the male (Fig. 43-44).

b) In the Female

The Vagina and Uterus (Fig. 46-47). The major portion of the vagina, all of the uterus, including the uterine horns, and the fallopian tubes are invested by the peritoneum.

There is a substantial nervous and vascular uterovaginal system which is not known in detail.

In the female examined by Hein (1914), the vagina was 40 cm long and had longitudinal folds. It was 5.5 cm in diameter and rich in mucus. Close to the external vaginal opening, the vaginal folds

Fig. 46 — Schéma d'une coupe longitudinale (moitié droite, vue du côté gauche) du vestibule vaginal, de la vessie et du rectum du Narval: CU : corne utérine; O : ovaire; M : mésentère; R : rectum; FRU : fente recto-utérine; Ur : uretère; P : pli vésical transverse; V : vessie; OU : orifice urétral; OV : orifice vaginal; A : anus; U : utérus.

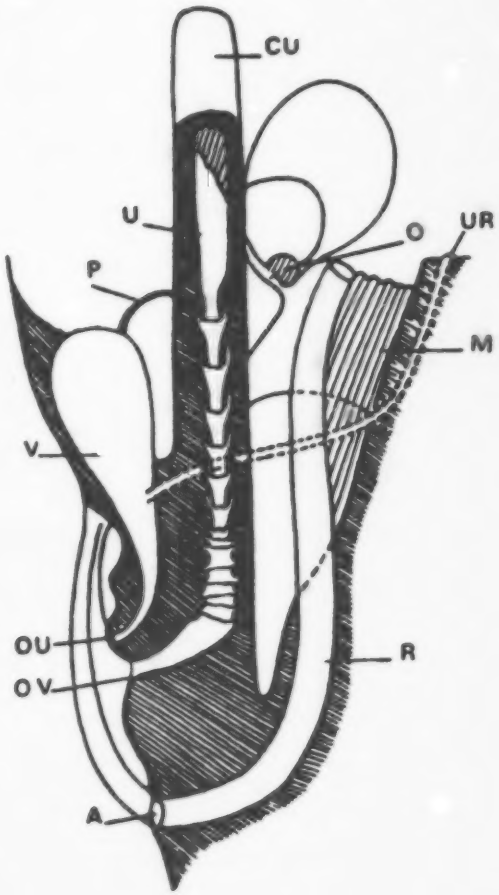

Fig. 46. Longitudinal section (right half seen from the left side) of the vestibule of the vagina, bladder and rectum. CU = horn of uterus; O = ovary; M = mesentery; R = rectum; FRU = rectouterine cleft; UR = ureter; P = transverse vesical fold; V = bladder; OU = orifice of urethra; OV = vaginal orifice; A = anus; U = uterus.

were grayish white, like the skin, on the elevated portions, but the base of the hollows was dark red. Toward the interior, the folds increased in number and became blackish red. At a distance of 12 cm from the vaginal opening, there were shallow, narrow, lamellar, transverse folds which became wider and deeper. There were 14 of these folds in all. The vaginal mucosa, which lay between the transverse folds, was lamellar with the ventral lamellae higher than the dorsal lamellae. The vagina opened progressively into the uterine horns. The vaginal mucosa was whitish yellow, whereas the uterine mucosa was dark red with a greenish tinge. Toward the front, there was a septum between the left and right uterine horns which were asymmetrical. The lumen of the left horn was much larger than that of the right horn and the folds were more massive. The fallopian tubes were very narrow near the horns and had longitudinal folds.

See page 70 a.

Fig. 47. Ventral view of the female genital tract. I = median incisure between the two uterine horns; S = septum between the two horns; CU = uterine horn; MS = mesosalpinx; LL = broad ligament; V = bladder; GL = labium majus; C = clitoris; U = urethra; Va = vagina; P = perineum; A = anus.

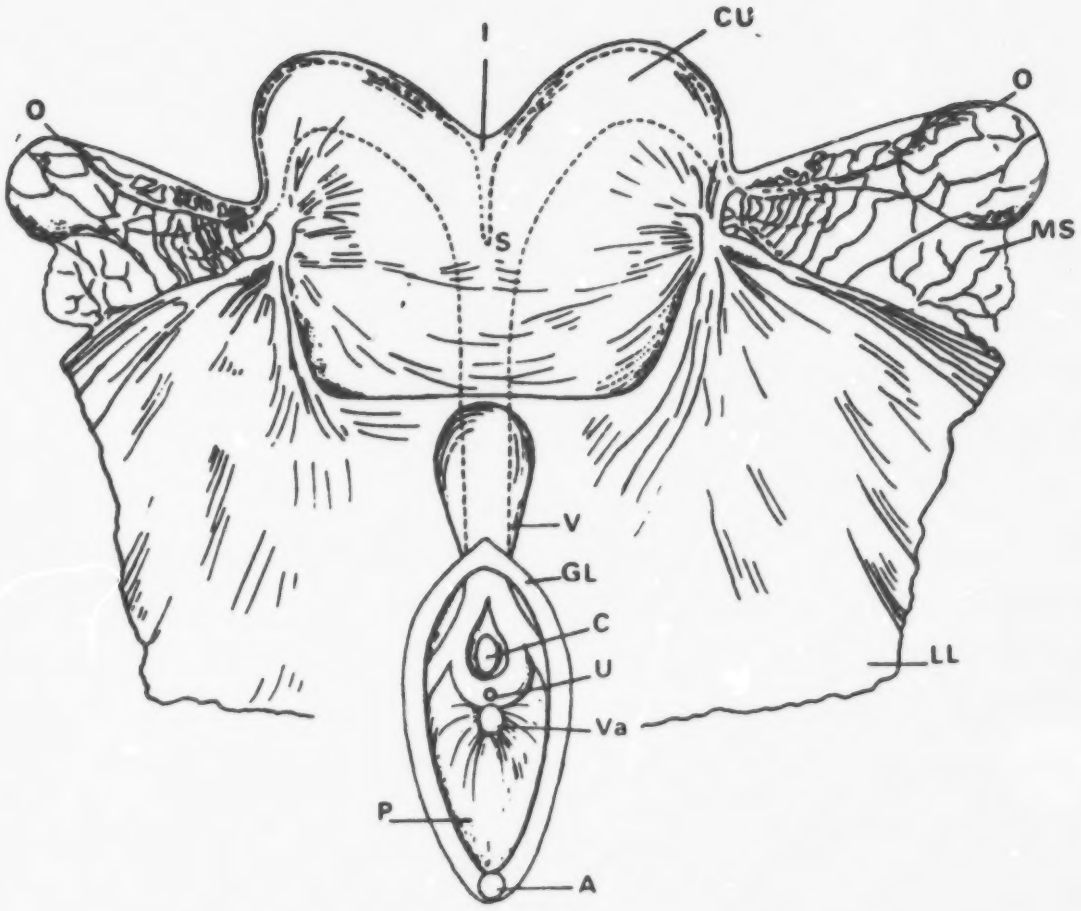

Fig. 47 — Vue ventrale du système génital ♀ du Narval; I : incisure médiane entre les deux cornes utérines; S : *septum* entre les deux cornes; CU : corne utérine; MS : mésosalpinx; LL : ligament large; V : vessie; GL : grande lèvre; C : clitoris; U : urètre; Va : vagin; P : périnée; A : anus

Fig. 47. Ventral view of the female genital tract. I = median incisure between the two uterine horns; S = septum between the two horns; CU = uterine horn; MS = mesosalpinx; LL = broad ligament; V = bladder; GL = labium majus; C = clitoris; U = urethra; Va = vagina; P = perineum; A = anus.

The Uterus and Placenta

Beginning in 1875, Turner examined several uteruses from gravid narwhals. In one specimen, the foetus was 5 feet, 5 inches long and located in the left horn. The gravid horn was 7 feet, 4 inches long, whereas the right horn along its greatest curve was only 4 feet long. The uterus was one foot in length and the vagina, 1 foot, 8 inches. The vaginal opening was occluded with an extremely viscous mucus plug.

The umbilical cord was twisted in a spiral. It was 3 feet long and contained two large arteries and two veins in addition to the urachus. The cord was joined to the abdomen midway between the anterior and posterior extremities of the foetus. It divided near the allantois, and the amnion formed a very large sac. The part of the amnion investing the cord had numerous brownish corpuscles, some of which were rod-shaped, whereas others were globular. Some were squamous. Others were not. The left horn, which was distended by the foetus, had displaced to the right the septum separating the two horns rostrally. The chorion extended from the gravid horn to the non-gravid horn, but appeared somewhat shrunk in size by the uterine septum. The chorion had thick longitudinal folds over the entire length of the non-gravid horn and the free end of the gravid horn. These folds offset a series of folds in the uterine mucosa that radiated from the orifices of the fallopian tubes. Deep folds in the mucosa also radiated from the uterine orifice far into the gravid chorion. The folds were as much as 3 inches deep in the mucosa. The part of the chorion that came in contact with this area of the mucosa was also lined with

folds. In the part of the gravid horn away from the foetus at the site where chorion and uterine stretch was maximal, no folds were observed. The entire chorion surface, with the exception of a few points, was covered with tightly packed vascular villi. The chorion adhered so closely to the uterine mucosa that traction had to be exerted to separate the two. When this was done, a multitude of open crypts which had been occupied by chorial villi appeared on the free surface of the mucosa.

The chorion opposite the uterine orifice differed from the above in that it was generally smooth with little vascularization and had only a few scattered patches of villi on the surface.

When examined under the cmicroscope, the villi, varying in number and size, were found to form clusters, some of which with only two or three villi. Usually, there were more, but occasionally a single villus occurred among the clusters. Most of the villi were racket-shaped but some were filiform. All were abundantly supplied with vessels and an extravillous layer of capillaries extended under the free surface of the chorion.

The surface of the uterine mucosa was delicately reticular and dotted with a multitude of recesses and grooves that were divided into countless crypts. In the polar areas of the uterine horns and the body of the uterus, the mucosa was softer and spongier than in the most distended portion of the gravid horn. Here the mucosa was stretched, and the furrows were virtually obliterated, with the crypts opening directly onto the mucosa surface. The crypts were

abundantly vascularized. They were lined with cylindrical epithelium in which the cells were occasionally as wide as they were high.

The uterine mucosa contains numerous glands that branch repeatedly. Some ramifications end in short diverticula; others are long. Some are straight, whereas others are twisted.

The chorial villi with crypts do not develop at the surface of the uterine mucosa until the embryo reaches a certain stage of development. They are certainly present when the embryo is 5 feet, 5 inches long, but do not exist in an embryo three-quarters of an inch long.

The Mammae

Like all cetaceans, the narwhal has mammary grooves near the genital cleft.

Howell (1930) examined a female foetus, 1.563 m long, and failed to find any sign of mamillae after he had drawn back the epidermal layer. Milk-bearing canals were clearly visible, however, directly dorsal to the vulva. They were roughly 2.5 cm long and were continuous with the lacteal reservoir (3 to 4 cm long). The latter extended to the front under the caudal margin of the internal oblique muscle of the abdomen. The walls of the lacteal reservoir were extremely thin and surrounded by finely granular tissue constituting the primordium of the mammary gland. There was no sign of differentiation of the caudal area of the panniculus into the future compressor muscle of the mamma.

Mammary glands are apparently not known in the narwhal. As in all cetaceans, the mammary grooves in this species are situated at the same level as the median urogenitoanal celft.

In a female foetus examined by Hein (1914), the median urogenital cleft was 35 cm long with the edges 5 cm apart. Two small grooves, 7.5 cm long, existed, one on either side of this cleft. The mamillae were invaginated in these grooves. The vaginal orifice was convex. There was a tiny external urethral opening with, in front, a button-like oval clitoris which was raised in a small cup-shaped depression.

5. BEHAVIOUR AND REPRODUCTION

"Even to this day a curious ignorance of the life of the narwhal persists, even among people living in the arctic regions; the truth is...that it lives in the Arctic world in large numbers."

Degerbøl and Frenchen, 1935

The narwhal, which is confined to Arctic waters, is the most polar of all northern cetaceans. It inhabits the edge of the polar ice. It rarely washes up on European shores. Only six times in the past three centuries have such incidents been reported. The first one occurred in the Ile of May in the Firth of Forth in 1648. A second narwhal was washed up in the mouth of the Elbe River in 1736. A third animal was stranded in Lincolnshire in 1800, a fourth in the Shetland Islands in 1808, and in 1949, two females were sighted, one at Rainham, the other at Medway.

Under normal conditions, narwhals head toward the coast of Greenland in winter, as far south as the 65th parallel. Pallas

spotted one off the coast of Novaya Zemlya and in the waters north of Siberia. In Canada, narwhals are regularly sighted off the east coast of Ellesmere Island, in Jones Sound and Lancaster Sound, in Prince Regent Inlet and Pond Inlet, toward Clyde River on the east coast of Baffin Island, and at Repulse Bay, north of Hudson Bay. Occasionally, they have been seen at Lake Harbour in Frobisher Bay, at Cape Dorset on Hudson Strait, at Coral Harbour on Southhampton Island and at Igloolik, north of Foxe Basin. They inhabit deep waters and overwinter in the open waters of Baffin Bay (Mansfield et al., 1975). Marcuzzi and Pilleri (1971) have given their range of distribution (Fig. 48).

See page 75 a.

Fig. 48. Distribution of the narwhal in the Arctic and North Atlantic. (After Marcuzzi and Pilleri, 1971; In Investig. Cetacea., 3, pp 117-8).

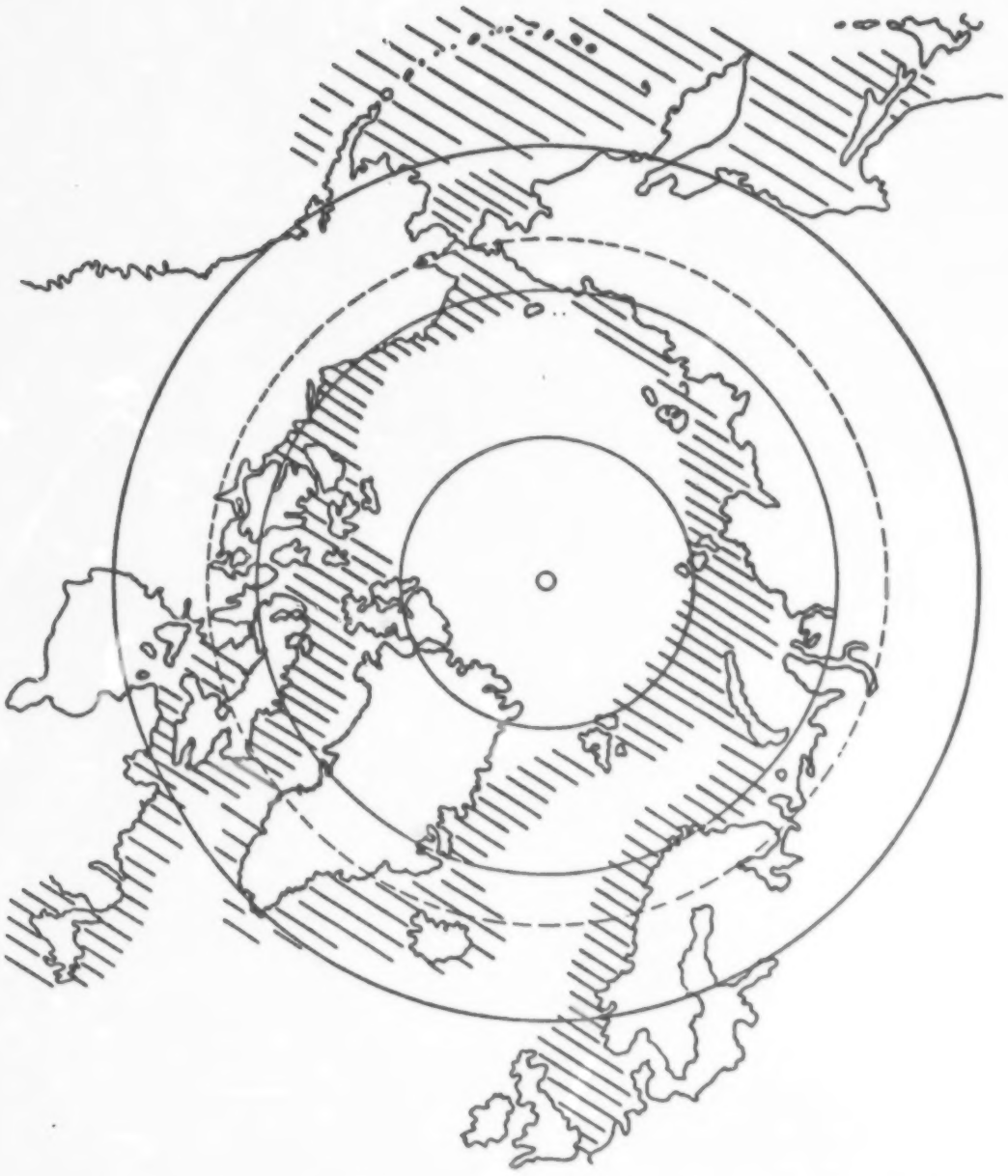

Fig. 48 — Répartition du narval, dans l'Arctique et dans l'Atlantique-nord, d'après Marcuzzi et Pilleri (1971), in : *Investig. Cetacea.*, 3, p. 117-8.

Fig. 48. Distribution of the narwhal in the Arctic and North Atlantic. (After Marcuzzi and Pilleri, 1971; In Investig. Cetacea., 3, pp 117-8).

Several naturalists have made attempts at counting the population. Tuck (1957) saw roughly 6,000 individuals north of Bylot Island in the course of the summer. Bruemmer (1971) sighted approximately 2,500 near Thule. In 1963, 442 narwhals were killed, and it may be assumed that there were twice that number because the hunters used guns before harpooning, with the result that many narwhals sank to the sea floor and were lost.

In 1663, La Peyrere stated that "the narwhal was to the whale what the rhinoceros was to the elephant" and as late as the 19th century, "natural cruelty" was said to be one of the attributes of the animal. Narwhals engaged "whales"in bloody combat, trying to skewer them with their "tusks" to kill them and savour "their tongues of which they were particularly fond." (Gérardin, 1817).

In actual fact, the narwhal is a peaceable cetacean and is rarely seen. Usually, the animals cluster into small groups, and only a few centimeters of their heads may be seen above the water. The rest of the body remains below the surface (Murdoch, 1917). Brown (1868), however, saw males and females together by the thousands in the open sea. Scoresby (1822) reported seeing them in herds of 15 or 20. It is not unusual to find a sleeping narwhal with just its blowhole above the water.

It is known that the animals cross certain bays or head for the mouths of certain rivers at set times of the year.

The left maxillary tooth is never visible except when the animal sleeps on its back or when males cavort about.

They are not mute but the sounds they produce have been diversely described. According to Murdoch (1917), their "groanings" may sound plaintive to our ears, but are undoubtedly due to the expulsion of air. These sounds may carry for some distance (up to 4 km) (Gorbunov, 1940). Degerbøl and Freuchen stated in their remarkable study (1935) that while the beluga produced "long, shrill siren blast-like" sounds, the narwhal produced the same sound "but quite briefly and just as it bops up out of the water; it appears to be made simply by forcing the air through the water in a certain manner"..."The shrill, whistle-like sound they make is sometimes relieved by a very short blast, with deep tones". The latter sound seems to be used especially by mothers calling their young. The off-spring stay close to their mothers for a long time. When they are very young, they breathe every 30 seconds.

Luckily, the sounds produced by the narwhal (from Baffin Island) have just been recorded under water by Ford and Fisher (1978). It is now clear that not only does the narwhal vocalize, but it also produces different sounds that have been recorded and analyzed. These sounds play a role in the species' social life as well as in echolocation and orientation.

When hunting, narwhals line up, side by side, in a single row, forming a sort of barrier from which their prey flees. Prey usually consists of cod, but in the autumn, narwhals prefer salmon trout. Before sounding, they line up, again side by side, in a single row, rather than behind one another and sound all at the same time.

Hunting isolated narwhal adults is far from easy. A solitary hunter has little chance of killing a narwhal which weighs over a tonne. Most often, the Eskimos hunt in groups of three, except in times of intense cold when the ice may trap the animals, forcing them to crowd near patches of open water to avoid asphyxiation. They are then easy to hunt. When the temperature of the air dips below - 20°C, moisture from the narwhals' expirations condenses and may be seen from afar. The Eskimos are thereby alerted to the presence of the water holes and come running. A number of polar naturalists have provided accounts of the massive and dramatic hunts that have taken place under these conditions. Egede (1721) was the first to describe how, in very cold temperatures, huge numbers of narwhals crowded in Disko Bay where they competed with one another for air and could not escape. Giesecke (1806), Rink (1852), Brown (1868), Vanhoffen (1897), Winge (1902), and Porsild (1915-1916) related in detail how the animals were hunted under these exceptional conditions which forced the narwhals to congregate at the water holes. During the winter of 1914-1915, a continuous sheet of thick ice formed far down to the south with the result that the narwhals had to crowd at rare sites where open water existed. Two hunts near Godhavn resulted in a kill of some 200 males whose maxillary teeth were planted

in the ice, marking the site (Fig. 49). It may be assumed that just as many females perished at this spot and sank.

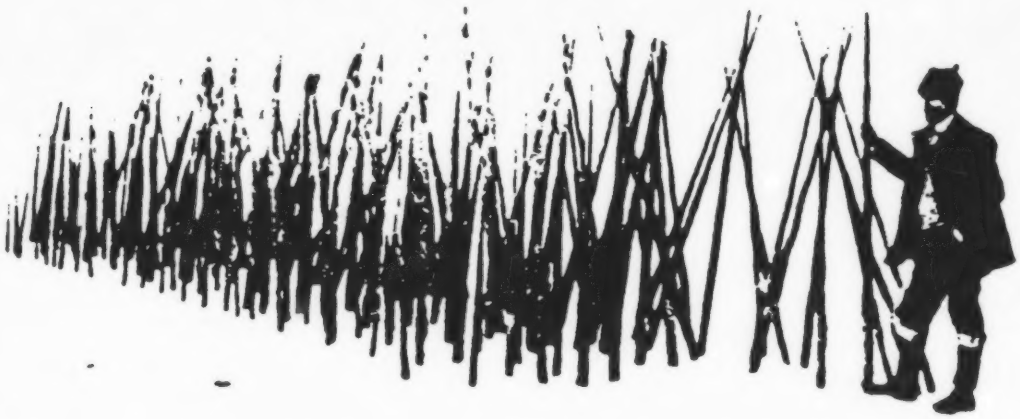

Fig. 49. Over 200 male narwhal teeth were planted in the snow after two "savssats" in which the animals, trapped in the ice and fighting for air, were easy prey for hunters. These two savssats occurred near Godhavn during the harsh winter of 1914-1915 (Porsild, 1918). Each expert hunter could kill 7 males a day and with the sale of only 5 teeth, which could be harvested in one day, made as much as a Greenlander working every day for 5 months.

In 1924, an ice hole in Admiralty Inlet (Siuraqtujuk) constituted an absolute trap. It was not any bigger than the area occupied by two tents, and more than 600 narwhals were crowded in the space. Some were lifted out of the water by others fighting for air in their agony. The males jostled their neighbours without ever attacking them with their maxillary teeth.

The Reproductive Cycle

Narwhals can mate at any time of the year. Foetuses of every stage of development are found throughout the year. Males, females and calves of all sizes often co-exist in the same herd. The animals mate in a vertical position (Brown, 1868).

The reproductive cycle is now well known as a result of research by Porsild (1922), Howell (1930), Pedersen (1931), Degerbøl and Freuchen (1935), Vibe (1950), Tomilin (1957), Sergeant and Brodie (1969), Brodie (1971), Bruemmer (1971), Best and Fisher (1975), and Mansfield et al (1975). Most calves are born during the warmest Arctic months, i.e., from the end of June to the end of August, when the fiords and bays are clear of ice. The gestation period lasts 14-15 months. The female gives birth every two (Vibe, 1950) or three years (Degerbøl and Freuchen, 1935).

Newborn narwhals range in length from 150 to 170 cm and weigh approximately 80 kg. They are nursed for approximately 20 months.

The females probably become sexually mature at about 5 years of age but apparently cease bearing young after 21 years of age.

Ovulation occurs more often on the left side, and the usually single foetus develops in the left uterine horn with its head toward the fallopian tube (Turner, 1875) and the tail toward the uterine orifice. The calves are born tail first (Pedersen, 1931). Degerbøl and Freuchen (1935) described the umbilical cord as "pearly."

Narwhal Prey

Narwhals seem to be voracious eaters. When in a favourable habitat, they will eat non-stop. In Eclipse Bay, Degerbøl and Freuchen (1935) found narwhals in which the stomachs and mouths were full of numerous small codfish, the size of a man's ring finger.

Narwhals are also known to eat flat fish, cephalopods (small cuttlefish, Gonatus, Rossia, Octopus) and other mollusks.

Stomach contents often include cephalopod beaks and otoliths from Boreogadus saida. In northwestern Greenland, most narwhals feed on Reinhardtius hippoglossoides, cod and shrimp (Vibe, 1950; Mansfield et al, 1975).

Narwhal Parasites

External Parasites

Parasitic infestations have rarely been reported in the narwhal, but Porsild (1922) found that animals from Disko Bay on the western coast of Greenland were often infested with Cyamus nodosus.

Paracyamus nodosus was identified in the narwhal by Lütken (1873), Margolis (1934) and Stephensen (1942). It is often accompanied by Cyamus monodontis (Lütken, 1870) or Cyamus ceti (Lütken, 1873).

Internal Parasites

The narwhal is apparently spared infestation from trematodes, cestodes or acanthocephalans (Arvy, 1977), but numerous nematodes have been identified in the animal:

Anisakis simplex, very common in the intestine (Diesing, 1851; Jägerskiold, 1893; and Baylis, 1932).

Halocercus monceris (Webster et al, 1973; MacNeill et al, 1975).

Porrocaecum decipiens (Delyamure; 1955).

Sternurus alatus (Baylis, 1916).

Terranova decipiens, an intestinal parasite (Baylis, 1916).

Torynurus alatus, frequent in the Eustachian tubes and lungs (Barbero and Thomas, 1960; Delyamure, 1968).

On dissecting the inner ear, Scoresby (1822) found large numbers of worms in the fat tissue. They were one inch long with unevenly pointed cone-shaped extremities. The worms were transparent with, internally, a canal-shaped structure. Externally, a brownish ridge ran along the entire length of the body.

The stomachs from narwhals killed in 1933 by the Eskimos of Rosenvinge Bay were found to contain unidentified nematodes (Tchernia, 1941).

Narwhal Diseases

It is not known what diseases afflict the narwhal. Calcium anomalies are apparently not uncommon. Cases of exostosis, which may have resulted from fractures, were studied by Slijper (1930). Eschricht had reported the existence of exostosis in a female specimen as early as 1838.

Nevertheless, the "royal mirror" condemned the consumption of narwhal flesh which was accused of being capable of transmitting some ill-defined fatal disease to man. It is known, however, that Greenlanders have consumed the meat since the dawn of time.

Narwhal Enemies

"Diese Fische* kann man nicht essen, weil man davon erkrankt oder stirbt, wenn man sie isst. Dieser Wall is nicht vom Wuchse gross; er wird nur 20 Ellen lang."

Guldberg, 1905, p. 33.

Man is a dangerous predator for the narwhal. In the Canadian Arctic along, an average of 150 animals are killed each year. In 1957 alone, 442 were killed, representing the largest number in any year for that area. In northwestern Greenland, 100 to 135 animals are taken each year. Wherever used, the methods for hunting the narwhal are open to criticism, and experts in the field estimate that roughly 50 % of the narwhals killed are lost. In the waters of Canada and Greenland, it is estimated that 900 births take place each year, but that a total of 1,154 narwhals disappear because of hunting practices. It became clear that something had to be done to restrict not only the areas where hunting could take place, but also the number of animals allowed per hunter. The natives of Pond Inlet, Clyde River, GriseFiord and Arctic Bay may not kill more than 5 narwhals a year per hunter. In addition, there are plans to introduce a limited hunting season and basically ban hunting in the narwhal's summer habitats and the use of excessively noisy boats (e.g., large motor boats, etc.) in these areas (Mansfield et al., 1975).

The restrictions placed on the consumption of narwhal meat in the Grágás or Speculum regale apparently are not followed today. Without elaborating, the Speculum regale advised against eating the flesh as it could transmit some fatal disease to man.

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* The narwhal

Apart from man, the killer whale (Orca) and walrus (Odobenus) are the narwhal's chief enemies. It escapes from the first by mounting on the ice (Degerbøl and Freuchen, 1935) and from the second by sounding (Fraser, 1937).

The Value of the Narwhal to Man

Narwhal meat is highly valued by Greenlanders both for themselves and for their dogs (Fraser, 1937). They prefer it raw and frozen. When high and even tainted, the meat acquires a pungent taste and smell which greatly appeal to the natives. The fresh fat is white, but becomes greenish with fermentation. The meat is dried in the sun for winter storage. Cutting it into cubes and strips makes it lose large amounts of its oil, just as drying eliminates much of the water. As a result, the meat decreases substantially in volumne.

Whole skin is considered a delicacy. It is referred to as "mattak" and is said to taste like hazelnuts. It is valued by the Greenlanders, just as bread is by the Europeans.

Narwhal oil is used as a source of heat and light. The skin is cut into thongs, straps and soles for shoes. The male tooth is used for harpoons.

The tooth no longer arouses any of the medicinal or even magic interest of days gone by. Powder from the tooth is obviously not endowed with power to combat poisoning (from arsenic, mercury and other heavy metals), and its value as a hemostatic in hemoptysis is just as

imaginary. It is unlikely that calcium from crushed teeth can be assimilated any better by decalcified subjects than, say, calcium lactate. Of all the virtues attributed to the narwhal, only one seems to be founded in reality and that is its effectiveness against scurvy. The disease is unknown among Greenlanders who consume large amounts of narwhal meat.

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